Sexual Selection in the Northern Fall Field Cricket, Gryllus pennsylvanicus: a Manipulation of the Adult Sex Ratio

by

Konstantine Souroukis

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ABSTRACT

The operational sex ratio has long been considered an important constraint on the structure of mating systems. The effects of an experimentally manipulated sex ratio on mating behavior and selection were investigated in a polygynous species, Gryllus pennsylvanicus, where the potential exists for spatial/temporal fluctuations in sex ratio of field populations. Four different sex ratios (males: females, 5:0, 5:2, 5:5, 5:10) were investigated. Observations were conducted in late summer over two field seasons, from 2400 h to 1000 h EST. Several male characters thought to be associated with male reproductive success were studied: calling duration, searching distance, weight, fighting behavior, courtship frequency, and mating success. Variance in male mating success was used as the indicator for the opportunity for sexual selection. Total selection was estimated as the univariate regression coefficient between relative fitness and the character of interest, while direct selection was estimated as standardized partial regression coefficients generated from a multiple regression of relative fitness on each character. The opportunity for sexual selection was highest at 5:2 and lowest at 5:10. The frequency of fighting behavior was highest at 5:2 and 5:5. Fighting ability (% wins) was determined to be an important correlate of male body weight. Direct selection for increased male body weight was detected at 5:2, while total selection for body weight was seen at 5:5. Selection on male body weight was not detected at 5:10. Calling duration decreased as sex ratio became more female-biased. Total and direct selection were detected for increased

calling at 5:2, only total selection for calling was seen at 5:5, whereas direct selection against calling was detected at 5:10. Searching distance also decreased as sex ratio became more female-biased, however no form of selection was detected for searching at any of the sex ratios. Data are discussed in terms of sexual selection on male reproductive tactics, the mating system and maintenance of genetic variation in male reproductive behavior.

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INTRODUCTION

Darwin (1871) proposed that sexual selection, the differential reproductive success of individuals of the same sex, could explain the evolution of sexually dimorphic traits. An understanding of the factors that affect the intensity of sexual selection will help elucidate the evolution of sexual dimorphism and the variation observed in mating systems. The contribution of population parameters towards the operation of sexual selection is fundamental, but population parameters are difficult to manipulate in a natural setting. Models indicate that population parameters are important towards the operation of sexual selection (Rowell and Cade, in press), yet empirical support is rare.

The operational sex ratio or the availability of reproductive males and females in a population (Emlen and Oring 1977), should influence male reproductive behavior and the intensity of sexual selection on males. As the number of females declines relative to males, intermale competition should become more intense, variance in male mating success should increase, and the intensity of sexual selection on male traits should increase. In species where males can assess female availability and vary their behavior accordingly, males should increase the amount of time and effort involved in competition for mates as the sex ratio becomes more male-biased (Emlen and Oring 1977). Spatial and temporal variations in adult sex ratios have been reported for a wide variety of species and should reflect life histories and ecological conditions. Such fluctuations might in turn lead to spatial and temporal variations in the intensity of

sexual selection in natural populations and contribute to the maintenance of additive genetic variation underlying male reproductive behavior.

Field crickets (Orthoptera: Gryllidae) offer a system where a population parameter such as the adult sex ratio can be manipulated while measuring the intensity of sexual selection. Previous field studies have shown that local population density greatly influences male field cricket calling and searching behavior and the resulting intensity of sexual selection on these male traits (French and Cade 1989; Cade and Cade 1992). Computer simulations of field cricket mating systems have demonstrated that the intensity of sexual selection should also vary with the operational sex ratio (Rowell and Cade in press). This particular study utilized the northern fall field cricket, Gryllus pennsylvanicus. The purpose of this research was to determine the effects of of an experimentally manipulated adult sex ratio on: (1) male and female behaviors which characterize the gryllid mating system; (2) the opportunity for sexual selection, using variance in male mating success as the indicator; and (3) the intensity of sexual selection acting on the male traits, calling duration, searching distance, and weight (a correlate of fighting ability).

LITERATURE REVIEW

In this section literature relevant to the thesis will be reviewed. The three areas focused upon are; selection, sex ratio and the behavior of Gryllus. These are broad topics which have been further subdivided. A brief introduction at the beginning of each section will outline the specific topics of this review.

Selection

This section begins with a brief history of how sexual selection has been treated by evolutionary biologists since its introduction by Darwin. It is followed by a review of some of the techniques used to measure selection. Included are concepts of fitness variance, partitioning of fitness into components, selection differentials and selection gradients. Next three problems that arise in the interpretation of selection gradients are presented. This section concludes with a brief review of Koenig and Albano (1987), an example of how the techniques discussed previously can be applied to study selection in a population of insects.

Natural Selection and Sexual Selection

Darwin (1871) clearly distinguished between natural selection and sexual selection. He believed that characters involved in the struggle for existence, such as efficient foraging behavior, were subject to natural selection, while characters used in competition among conspecifics for mates, such as courtship displays, were subject to sexual selection. Natural selection occurs when environmental and biotic factors cause variance in fitness of the genotypes, as expressed by phenotypes, present in the population.

This results in a change in gene frequency within that population across generations. Sexual selection consists of two primary components: (1) intrasexual competition where the members of one sex compete among themselves to mate with members of the other sex; and (2) mate choice where members of the non-competing sex show preferences based on fitness indicating attributes. These components result in differential reproductive success among individuals of both sexes, but more variance should be observed among individuals of the competing sex, usually the males (Trivers, 1972). Bateman (1948) showed that this was true for Drosophila melanogaster when he observed that the variance in the number of offspring left by males was greater than that left by females. This was mainly due to variance in the number of females mated by the different males.

For a number of reasons Darwin's theory of sexual selection received much criticism, which was followed by ridicule and then was subsequently ignored for decades. Julian Huxley (1938) wrote "None of Darwin's theories has been so heavily attacked as that of sexual selection". Some of his critics claimed that Darwin invented the theory of sexual selection because he was unable to to explain many human attributes as being due to natural selection (Mayr, 1972). A much more serious problem confronting sexual selection theory concerns Darwin's treatment of the concept of fitness. To Darwin fitness meant well adapted, and anything that improved the organism's chance for survival. Fitness in the Darwinian sense was a property of the individual or, as employed today, the genotype (Mayr, 1972). The "forgotten era" of sexual selection began in the

1930s when the mathematical geneticists (Haldane, Wright and Fisher) redefined fitness as a change in gene frequency (Mayr, 1972; West-Eberhard, 1983). They introduced the concept of the fitness of single genes. Fitness under this new definition could be due either to superior fitness in the Darwinian sense or reproductive advantage that does not add to the adaptedness of the species to its environment. This new definition facilitated the use of mathematical models in evolutionary theory, but trivialized the theory of sexual selection. It now became a subcategory of natural selection (Mayr, 1972).

The "forgotten era" of sexual selection coincided with the "golden era" of neo-Darwinian speciation theory (West-Eberhard, 1983). As a result sexual selection theory played almost no role in modern ideas of speciation. This was unfortunate because speciation theory at this stage involved concepts such as the importance of geographic isolation in promoting divergence (Mayr, 1963), and the importance of courtship and pre-mating signal divergence in effecting reproductive isolation (Alexander, 1962). Clearly, sexual selection theory could have contributed much to the understanding of these concepts (West-Eberhard, 1983).

More recently, biologists began to explore the question: "Is it possible to make a sharp distinction between natural selection and sexual selection, as claimed by Darwin and Huxley?" And if sexual selection does exist, what forms does it take, how widespread is it, and what kinds of characteristics can be attributed to it (Mayr, 1972)? Darwin believed that sexual selection usually resulted in sexual dimorphism, but that not all sexual dimorphism was due to

sexual selection. Darwin believed that sexual characters such as claspers which facilitate copulation, and the cryptic coloration of female birds and female butterflies, were sexual dimorphisms due to natural selection. What characters are due to sexual selection then? The bright coloration of many male birds and the special plumes of peacocks and of birds of paradise were traits that were genuinely the products of sexual selection. "It is clear that these characters are the result of sexual and not of ordinary selection, since unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving numerous progeny, but for the presence of better endowed males" (Darwin, 1859).

Gradually sexual selection theory received increasing attention in the fields of animal behavior (Trivers, 1972), mating systems (Emlen and Oring, 1977) and speciation (Lande, 1981; Kaneshiro and Boake, 1987). A great many modern researchers, however, do not use the term sexual selection as it was defined by its originator. Since all traits affect gene transmission, a trait that is correlated with survival will persist only if survival is correlated with reproductive success. Sexually selected traits are often negatively correlated to longevity. Predators may orient towards sexual signals, which are sexually selected traits, consequently decreasing the probability of survival for signalling individuals. Such decreased survival, however, can be more than compensated for by the higher numbers of mates encountered by signallers. Thus sexual selection should be treated as a subcategory of natural selection (Otte, 1979). Both will affect the evolution of the sexual signal to increase fitness (Alexander and Borgia, 1979; Thornhill and Alcock, 1983).

Sexual selection has been proposed to explain extraordinary sexually dimorphic characters at variance with Darwin's concept of natural selection (Arnold, 1983). Arnold writes "The key to seeing Darwin's distinction between sexual and natural selection is to focus not on the variety of sexually selected characters, but instead to consider the effects of such characters on fitness. Characters that evolve by sexual selection are those that cause differences, or variance, in male mating success." Thus sexual selection arises from variance in mating success while natural selection arises from variance in all other components of fitness. Arnold (1983) calls this a "statistical view", a view that once adopted has two advantages: (1) one need not identify the agent of sexual selection in order to measure it; and (2) the intensity of sexual selection can be measured with conventional statistics, using reproductive success as the indicator.

Measuring Sexual Selection

The most comprehensive set of tools for measuring sexual selection are those provided by the "Chicago School" (Grafen, 1988). This body of literature includes the papers Wade and Arnold (1980), Lande and Arnold (1983) and Arnold and Wade (1984a and 1984b). The model proposed by these authors is probably the most widely accepted and utilized method for measuring sexual selection. The wide acceptance of this model is probably due to the fact that it uses variance in reproductive success to measure selection. The concept of fitness variance has been influential in evolutionary biology since it was introduced by R. A. Fisher (1958). Sutherland (1985) developed an alternative model based on search-time for mates. The essence of

this model is described by Sutherland: "I shall assume that the strength of sexual selection is the degree to which different phenotypes have different fitnesses due to differences in the frequency or quality of mates". In the actual model he ignores the mate quality aspect and just considers the extent to which different phenotypes differ in mating rate. This model seems to overcome some shortcomings of the previous model, but has yet to attract widespread empirical enthusiasm.

Crow (1958) noted that the expression for the change in mean fitness each generation is mathematically equivalent to the product of fitness heritability and the variance in relative fitness. He called the variance in relative fitness the intensity of or opportunity for selection, since it limits the rate of evolution (Arnold, 1983). The next major advance in measuring sexual selection took some time to realise. Wade and Arnold (1980) proposed that total fitness of an individual could be represented as the product of fitness components. The main advantage in partitioning relative fitness in this manner is to identify the component(s) on which selection may be operating. There is no difference between sexual selection and natural selection in the methods of measurement or of demonstration (Arnold and Wade, 1984a, b; Endler, 1986). In many cases, researchers attribute particular fitness components to either natural selection (longevity) or sexual selection (mating rate), thus enabling one to measure the separate forces of natural and sexual selection so that they can be directly compared. The importance of making such distinctions and comparisons is not entirely clear, especially in light

of the fact that the phenotypic consequences of natural selection and sexual selection are not so easily distinguishable.

Estimating fitness of individuals is necessary, but not enough to detect selection. One must also collect data on phenotypic traits suspected of being the targets of selection. The simplest way to detect selection is to regress total relative fitness onto the phenotypic trait in question. The slope of a univariate regression of this nature is a measure of selection intensity and is termed the selection differential (Falconer, 1981). Another way to estimate the selection differential is to obtain the covariance between total relative fitness and the character (Lande and Arnold, 1983). The selection differential measures total selection on a trait, total selection being the sum of direct selection, plus indirect selection contributed though correlated characters. The selection differential plays a key role in equations that predict evolutionary change. In order to predict evolutionary change (the response to selection that occurs across generations), however, information about the inheritance of the trait is required (Arnold, 1983). The expected change in the mean of the character from one generation to the next is the product of heritability and the selection differential (Falconer, 1981). Although response to selection is certainly a useful tool predicting evolutionary change, selection itself is a within-generation, phenotypic event, and therefore, no knowledge of heritabilities is required to measure selection (Arnold, 1983).

Perhaps a more useful way of analyzing selection is through multivariate statistics. Selection gradients are generated as standardized regression coefficients from a multiple regression

relating the fitness estimate to the characters of interest. In this way, estimates of direct selection on specific traits can be obtained if all correlated traits are entered into the analysis. This is the primary advantage to using such multiple regression analysis. The multiple regression will generate the best-fitting, straight line, relating fitness to each character individually by holding the effects of all other characters constant (Lande and Arnold, 1983). Although the selection gradients are useful in identifying the targets of selection, they cannot be used to predict evolutionary change, because total selection, rather than direct selection, is what dictates the evolutionary response of characters.

Three problems arise in the interpretation of selection gradients (Grafen, 1988). The first problem concerns the omission of relevant characters. It is not always possible to collect data on every character which may be relevant to reproductive success. For example, a character included in the multiple regression might be influenced by pleiotropic loci with obscure effects. Another way in which relevant data could be missed is through what Grafen calls the "silver spoon effect". He defines this as positive correlations between characters in the adult that are also positively associated with fitness. They are brought about by the common underlying cause of favorable or unfavorable, and often, unobserved environmental effects during development. Furthermore, data omission could also result from the fact that observable differences in behavior may be consequences of unobservable differences in health or vigor that are the true causes of variation in reproductive success. The second problem concerns the quantity of natural variation in characters. A

selection gradient not significantly different from zero may be the result of the character being selectively irrelevant or the result of the character not having enough independent variation. If natural variation is small, large samples are needed in order to detect an effect that genuinely exists. The third problem concerns incomplete data sets which many times result from early mortality preventing the measurement of important characters in adults. For example, a male may have a faster growth rate than another, but only by allocating more energy towards growth instead of defense against disease. So the "largest" males may die as juveniles and do not have their adult size measured. These individuals should appear in the multiple regression but often do not.

Although some problems exist with the interpretation of selection experiments, tremendous insight can be gained through the discriminating biologist. Koenig and Albano (1987) measured the opportunity for selection and selection on several morphological and behavioral traits for both sexes. They estimated lifetime reproductive success in the territorial dragonfly, Plathemis lydia. There are two general methodologies that are commonly used in studies of selection: cross-sectional experiments, where a relatively small proportion of the lifespan of individuals is considered, and longitudinal studies, where lifetime reproductive success is estimated. The cross sectional design is often used to look at single selection events under different conditions and therefore explores questions concerning the operation of selection. Longitudinal studies often address questions concerning the importance of the different episodes of selection relevant to particular taxa. Lifetime

reproductive success may be the best measure of fitness that can be collected (Clutton-Brock, 1988), but it is difficult to obtain such data in many species. Koenig and Albano (1987) is a longitudinal study. Selection can be measured for both sexes, but it is often more difficult to obtain reliable data for female insects because of sperm competition and cryptic oviposition behavior. However, for some species like Plathemis lydia, fairly reliable techniques have been developed. Koenig and Albano defined total fitness for males as number of eggs fertilized, while for females, total fitness was seconds of oviposition. They partitioned male fitness into 6 components and female fitness into 3 components. One advantage in being able to partition fitness is that some components are mainly attributable to natural selection, while others to sexual selection. In Koenig and Albano, longevity, estimated as days alive, is subject to natural selection, while matings per hour present is largely attributable to sexual selection. Another advantage of this method is that the opportunity for selection and selection on traits can be measured at each selection episode. Koenig and Albano tested for selection on four characters: first date of reproduction, body mass, hind wing length and relative time spent in flight by territorial males. The only selection detected in this study was for early reproduction in males, and this was primarily due to increased survivorship and increased time per day spent at the pond. Selection differentials and selection gradients can be used to identify the target of selection, while division of selection into episodes is useful in identifying the source of selection. Although problems exist with the interpretation of selection experiments, the data obtained from such studies can

become very informative if the advantages and disadvantages of these techniques are considered and discussed.

Sex Ratio

This section begins by defining sex ratio and then leads into a discussion of selection on sex ratio. This is followed by a brief review of some mechanisms that may generate sex ratios which deviate from unity. Finally, several important studies dealing with the effects of different sex ratios on behavior, selection and mating systems, are reviewed in some detail.

Definitions and Selection on Primary Sex Ratio

The numerical relationship referred to as sex ratio is the proportion (or percentage) of males in the population. This relationship is highly dependent on the life history characteristics of a particular species, so it is worthwhile to make at least 4 distinctions. (1) The primary sex ratio is the ratio at the time of fertilization. It is not practically accessible to observation in most species; (2) the secondary sex ratio is the ratio at birth, hatching or any other appropriate emergence into the pre-reproductive condition; (3) the tertiary sex ratio is the ratio at the time of sexual maturity; and (4) the operational sex ratio is "the average ratio of fertilizable females to sexually active males at any given time". This concept was devised because in order "to understand the intensity of sexual selection, it is not the overall population of males to females that is important, but rather what we term the operational sex ratio". The operational sex ratio indicates the degree of monopolization of mates. When one sex becomes a limiting factor for the other, the result is an increase in intrasexual competition among members of

the available sex for access to mates of the limiting sex. The greater the imbalance, the greater the variance in reproductive success among members of the available sex, and the greater the degree of polygamy (Emlen and Oring, 1977).

Fisher's (1958) theory of equal parental investment in sons and daughters explains why tertiary sex ratios of unity are commonly observed in natural populations. In large outbreeding populations, equal effort and resources should be allocated to each sex because each of the two sexes contributes equally (genetic material) to the next generation. In a wide variety of organisms the observed sex ratio is unity, thus the average reproductive value of males is equal to that of females. If sons become more costly to raise, then proportionally more daughters should be produced so that the overall population expenditure on each sex remains the same. Hamilton (1967) showed that female biased sex ratios would be favoured where male siblings compete for mating opportunities, a situation he referred to as local mate competition. Local mate competition theory has been expanded to deal with co-foundresses with different clutch sizes. Such cases are applicable to parasitoid wasps where double parasitism often occurs. It was determined that the more fecund female should always produce the more female biased ratio. Local mate competition theory explains the female skewed sex ratios of many hymenopterans and has been modified further (variable maternal condition) to deal with the aphid system (Yamaguchi, 1985). Many social spiders also show female-biased sex ratios, and in many of these systems, levels of inbreeding and local mate competition are thought to be high (Frank, 1987).

Trivers and Willard (1973) proposed that in polygynous species with maternal care, healthy females should male-bias offspring production, while females in poor condition would benefit by female-biasing their offspring production. The reasoning being, that because males realize greater variance in mating success than females, a healthy mother gains by raising healthy, strong sons who should prove quite successful under polygyny. Sons produced by an unhealthy female, in contrast might not fair well in this type of mating system, but because nearly all females are able to mate under polygyny, such unhealthy mothers should therefore female-bias their progeny. Thornhill (1979) proposed a similar argument for a polygynous mating system, based on the genetic quality of the mating male. Females mating with high quality males would benefit by producing more sons. On the other hand, if the male was of low quality, females should produce more daughters. Falconer (1954) performed 3 artificial selection experiments (on Drosophila and mice) in an attempt to show additive genetic variation for sex ratio. He concluded by stating that the absence of detectable additive genetic variance for sex ratio suggests that the underlying genetic control for sex ratio may differ from better known quantitative characters. Shortly after Falconer's paper appeared, the segregation distorter gene was discovered in Drosophila melanogaster by Hiraizumi (reviewed by Crow, 1979), and since that time several other mechanisms by which sex ratios can deviate from unity have been reported.

Evidence for Sex Ratio Deviation from Unity

There are 4 ways in which sex ratios can be altered from the Fisherian 1:1 ratio: (1) aberrant meiotic segregation; (2) gametic selection; (3) zygotic selection; and (4) post zygotic selection. The first two mechanisms operate through the additive effects of constituent families and affect primary sex ratios. Zygotic selection would affect secondary sex ratios. Post zygotic selection includes all forms of selection commonly observed and would affect tertiary and operational sex ratios.

Aberrant meiotic segregation is one mechanism by which the constituent broods of a population can become sex ratio biased. Overall population sex ratio might be affected depending on how the constituent families are represented. Meiotic drive systems on the sex chromosomes appear to be rare in nature. Hamilton (1967) suggested that one reason the Y chromosome is so devoid of genes in many species is that the lack of genes prevents meiotic drive mutants from arising and wiping out the population (through the absence of one sex within a few generations). Segregation distorter in D. melanogaster can exclude 99% of the competing allele (reviewed by Crow, 1979). If a segregation distorter complex were to be placed on the Y chromosome, nearly all of the progeny would be expected to be males. This is exactly what happened in repeated laboratory experiments using translocated male Drosophila. Furthermore the experimental populations went extinct within a few generations due to the lack of females (reviewed by Crow and Dove, 1988). Craig et. al. (1960) described a meiotic drive gene near the male-deteriming gene in the yellow fever mosquito, Aedes aegypti. This system

contains many modifying genes so that the effect of the distorting gene is rather mild. A meiotic drive system is known to contribute to the female-biased sex-ratios in wood lemmings, Myopus schisticolor (Bull and Bulmer, 1981) and has been implicated in contributing to the female biased primary sex ratio in the solitary spider, Pityohyphantes phrygianus (Gunnarsson and Andersson, 1992).

Haldane's rule states that "when in the F1 offspring of a cross between two animal species or races, one sex is absent, rare or sterile, that sex is typically the heterogametic sex" (Haldane, 1922). Frank (1991) proposed a model to explain Haldane's rule, whereby a system of diverged sex chromosomes containing meiotic drive elements are reintroduced. The model essentially states that suppressor genes keep distorting genes in check. If the population diverges, novel random mutations may occur at the distorter loci in one or both populations. Within populations, suppressors would quickly evolve to counteract the effect. Upon hybridization, however, incompatibilities between the systems would manifest as meiotic drive (absence of the heterogametic sex). One important implication of Frank's model is that meiotic drive systems on sex chromosomes may by quite common, yet their effects may be difficult to observe. If meiotic drive systems are widespread, acting in a mild fashion through the constituent families of a population, they could make significant contributions toward temporal and spatial sex ratio heterogeneities within populations.

Gametic selection would produce similar effects to aberrant meiotic segregation if gametes containing X and Y chromosomes (in the case of heterogamety) possessed variance in the ability to

achieve fertilization (Colaianne and Bell, 1970). Gametic selection, however, would operate after the time of gamete formation and up until the time of fertilization. Although this generally manifests as competition between gametes of the same parent, an increased level of complexity is added when a species multiply mates. Elements of sperm competition must then be considered. Evidence for gametic selection in species where internal fertilization occurs is rare. And to go even further, to demonstrate that such a phenomenon could contribute to sex ratio heterogeneities at the population level would be a difficult task, even though the mechanisms may exist.

A variety of isopods and amphipods display a phenomenon which has been termed monogeny, whereby a proportion of females produce either male-dominated (arrhenogenic) or female-dominated (thelygenic) broods, while others produce unbiased broods (amphogenic). In these organisms maternally-inherited intracellular micro-organisms transmitted via the oocytes, and nuclear factors, override the mechanism of chromosomal sex determination, and result in monogeny (Bull, 1987; Heath and Ratford, 1990). This type of phenomenon could be classified as a type of environmental sex determining mechanism. The zygotes are "transformed" in response to the early embryonic environment. No selection on gametes or zygotes occurs here.

Certain female Hemipterans such as the southern green stinkbug, Nezara viridula, are capable of adjusting their offspring sex ratio in response to population structure. Female stinkbugs initiating copulation in a female biased environment produce relatively more sons than females initiating copulation in a male-biased

environment. After factors such as differential mortality and female condition were ruled out, it appeared that female stinkbugs were capable of facultative sex ratio adjustment in response to the operational sex ratio, increasing the production of sons when males are rare. The proximate mechanisms of this phenomenon are not known (McLain and Marsh, 1990).

In red-winged blackbirds, the sex-ratio of offspring leaving the nest varies with maternal age. Young mothers produced nearly twice as many daughters as sons, middle aged mothers produced equal proportions of sons and daughters, and old mothers produced significantly more sons. Furthermore the secondary sex ratio (at hatching) of old mothers was significantly male biased (Blank and Nolan, 1983).

Zygotic selection may act against either male or female zygotes at any time between fertilization and the attainment of adulthood (Colaianne and Bell, 1970). Differential mortality between the sexes gives rise to skewed sex ratios. The "sonless" sex ratio anomaly in D. melanogaster is a case of zygotic selection whereby individual broods become female-dominated. Though not apparent initially, this was demonstrated to be a case of zygotic selection because sons were shown to die during embryonic or early larval development. Zygotic selection can be caused by cytoplasmically transmitted infectious particles as well as nuclear genes (Colaianne and Bell, 1970). Zygotic selection affects secondary sex ratios, in contrast to aberrant meiotic segregation and to gametic selection, which both affect the primary sex ratio.

Post-zygotic selection, on the other hand, involving the forms of natural and sexual selection most commonly observed, acting differentially on the sexes, can affect tertiary and operational sex ratios. Such variance may arise though differential longevity, predation, parasitism and even chance events if the sexes occupy different microhabitats, or possess a variety of dimorphisms (cryptic vs. bright coloration or displaying vs choosing). In species where males signal or display to attract cryptic females, spatial and temporal sex ratio heterogeneities on a local scale might develop, through sex biased predation and parasitism. Walker (1964) observed a cat stalking a calling katydid. Orthopterans and cicadas are excellent examples of where such spatial and temporal sex ratio heterogeneities might develop because generally it is the males that signal acoustically. Gwynne (1987) found that more males than females of the tick-tock cicada, Cicadetta quadricincta, were captured by web-building spiders. This example of sex-biased predation appeared to be a consequence of male mate-seeking activities, but it was not the result of males calling but rather due to the short flights made by males when responding to the signal of receptive females.

Sex Ratio, Behavior, Selection and the Mating System: Empirical Studies

Emlen and Oring (1977) hypothesized that the operational sex ratio is one of the primary forces shaping mating systems. As the operational sex ratio becomes skewed, polygamy should become more pronounced, competition within the more abundant sex should intensify and variance in reproductive success within the more abundant sex should increase. These are important predictions that

require empirical clarification. Thornhill (in Thornhill and Alcock, 1983) tested these predictions in caged populations of the scorpionfly, Panorpa and he found that variance in male mating success increased as the sex ratio became more male biased.

Empirical studies involving natural populations, in which sex ratio manipulations have been attempted are not common. The main problem lies in the difficulty of conducting such trials in natural environments, whilst minimizing investigator disturbance, thus most are conducted in controlled enclosures or under pseudo-natural conditions (for example; Thornhill's Panorpa experiment). Another direction in which the empiricist could approach the problem from is to utilize the natural variation in sex ratio. One major drawback in using this approach is that it is difficult to interpret numerical sex ratio data from sampling natural populations. Problems arise from sex dependent differences in behavior, which could make accurate estimates of natural sex ratios very elusive. This approach would also require the removal of effects by many confounding factors (spatial vs temporal heterogeneity) before any meaningful conclusions could be drawn.

Even though rigorous quantitative sex ratio data from the field are limited, sex ratio manipulations have been attempted in pseudo-natural environments. In the large, monogamous, Midas cichlid, Cichlasoma citrinellum, polygamy could not be induced by manipulating the sex ratio (Rogers, 1987). This species inhabits the Great Lakes region of Nicaragua, where breeding sites are limited and breeding success can be quite low. The experiment was essentially a test of the strength of the pair bond. Sex ratios of 1:1,

2:1, 4:1, 1:2 and 1:4 were used. As the sex ratio deviated from unity, the breeding success of those pairs that formed decreased. Rogers' results indicated that the Midas cichlid is obligated to monogamy because both parents are needed to defend the breeding site as well as the subsequent fry. Although the sex ratio manipulation could not alter the mating system, behavioral changes were observed and they primarily involved increased levels of male-male aggression as crowding increased. Rogers' work indicated that life history characteristics and ecological constraints are important variables, important enough to counteract the predicted effects of manipulated sex ratios.

Kordic-Brown (1988) demonstrated that the operational sex ratio of pupfish, Cyprinodon pecosensis, affected the proportion of males adopting primary and secondary breeding tactics as well as the intensity of sexual selection. Pupfish are annual and have a single breeding season, during which the males acquire bright coloration, while females remain cryptic. Both sexes are promiscuous and there is no parental care. Male reproductive success is determined by access to females, whereas female reproductive success is limited by the number of eggs produced.

Kordic-Brown manipulated sex ratio by varying the number of females. The spawning success of breeding males was directly related, and the intensity of male-male competition was inversely related, to the number of females. In the male biased treatment, males engaged in a greater number of agonistic interactions and fewer courtship bouts. In the female biased treatment, courtship behavior became more frequent than agonistic behavior. A greater

proportion of males adopted the satellite breeding tactic in the male biased and the even sex ratio treatments. Smaller, competitively inferior males were more sensitive to changes in sex ratio. As the sex ratio became more female biased, average male mating success increased and some of the satellite males were able to adopt the territorial breeding tactic. This is an important study because it was perhaps the first to demonstrate that temporal and spatial changes in the operational sex ratio may have profound effects on the mating system. The predictions made by Emlen and Oring (1977) appear to be supported by this Pecos River pupfish system.

Gwynne (1990) tested the hypothesis that variation in parental investment controls the number of females and males available for mating in Requena verticalis, a listroscelidine katydid from Western Australia. Males of this species produce a spermatophore which consists of a sperm ampula and a spermatophylax. A few minutes after copulation, the female removes the spermatophylax from the spermatophore and consumes it over a period of about 5 hours. In R. verticalis, the spermatophylax nutrients are largely translocated to the eggs and increase both fecundity and the weight of the eggs produced (Gwynne, 1984). The sperm ampula takes about 2.5 hours to drain and when the female is finished eating the sprematophylax she may remove the sperm ampula from her gonophore and consume it as well. Males are thought to invest heavily in spermatophores because it takes them about 5 days to produce another. The average remating interval for females is only slightly less (about 4 days). This species does not show the sex role reversals observed in the mormon cricket or some of the other katydids, but

there is some evidence that males show mate rejection. Gwynne (1990) stated that detailed information about variation in mating behavior is not available for this species.

In Gwynne's study, male and female katydids were maintained on diets that differed in food quality. Both sexes were given daily access to sexually receptive members of the opposite sex. Males on a low quality diet mated less frequently than males on a high quality diet. Conversely, females on a low quality diet mated more frequently than females on a high quality diet. In males, the availability of food determines the frequency of spermatophore production and thus the number of males available for mating. Poorly nourished females, on the other hand, mated more frequently, apparently obtaining nutrients through spermatophores. The effects of diet on the mating system would be: (1) when diet quality is high, there are fewer fertilizable females than sexually active males, resulting in male-male competition and polygyny; and (2) when diet quality is low, there are only slightly fewer fertilizable females, resulting in female-female competition. Gwynne (1990) has shown that diet quality affects the relative importance of male and female parental investment in this katydid, which in turn results in different numbers of males and females available for mating. In short, ecological factors can, to some extent, determine the operational sex ratio, which in turn shapes the mating system.

A North American water strider, Gerris remigis, copulates for prolonged periods of time (on the order of several hours). The duration of copulation is beyond the time required for insemination (Clark, 1987). Clark (1988) tested the hypothesis that prolonged

copulation functions as a type of contact mate guarding, which reduces sperm competition by preventing the female from remating prior to oviposition. He demonstrated in laboratory streams that when the population was male-biased, males copulated for significantly longer periods of time. This result supports the mate guarding hypothesis and demonstrates that the operational sex ratio has profound effects on mating behavior and on the structure of the mating system.

A competing hypothesis is that female G. remigis prolong copulation because it increases female foraging efficiency. Gerris females generally channel food into specific regions, and then defend their food rich areas. Female G. remigis have been observed to copulate and forage in the same areas and often concurrently. Wilcox (1984) found that when males were present, female G. remigis could forage efficiently only by being in copula, single females were chased by ardent suitors and thus showed decreased feeding times. Clark (1988) also tested the female foraging hypothesis by manipulating the period of food deprivation in females. In this experiment, he held sex ratio and population density constant. The prediction here was that starved females should copulate for longer periods than fed females. However, no significant difference was detected between the two groups. Clark concluded that only the copulatory guarding hypothesis was supported, but there may be a selective advantage to female foraging which helped drive the evolution of prolonged copulation.

Arnqvist (1992) provided an empirical test of the relationship between the intensity of selection and sex ratio in the water strider,

Gerris odontogaster. In this species, the sexes engage in a precopulatory struggle. Females often dislodge mounting males, while males have evolved two abdominal processes, which enable them to grasp females during mating and help prevent dislodgement. Males with longer processes are more successful because they grasp females tighter. When the sex ratio becomes male-biased females become less discriminatory, thus the operational sex ratio should then be negatively correlated with the importance of longer abdominal processes. Arnqvist (1992) found that the relative mating success of males with long abdominal processes did indeed decrease with increasing sex ratio (males/total). These results are in general disagreement with sexual selection theory; it appears that the intensity of sexual selection is negatively correlated with the operational sex ratio. This discrepancy arises from the fact that female G. odontogaster alter their behavior as the sex ratio changes. This paper is important because it shows that the relationship between sex ratio and the intensity of sexual selection is not straightforward: it may be influenced by changes in the behaviors of the sexes (Arnqvist, 1992).

The milkweed beetle, Tetraopes tetraophthalmus, is sexually dimorphic with larger females than males. Prolonged matings and multiple matings occur. Females lay small clutches repeatedly throughout their lives. Lawrence (1986) showed that male milkweed beetles not only exhibit mate choice but also exhibit direct competition for access to mates. Naturally occurring sex ratios show pronounced spatial and temporal variability and this variation occurs

on the time scale of a single copulation (several hours). Females of this species often clump together.

Lawrence (1986) showed that males become increasingly choosey when the sex ratio is female biased (<1:1.25), and more competitive when the sex ratio is male biased (>1.25:1). Larger males win most aggressive encounters, and males generally prefer to mate with larger females. Females do not appear to choose or compete. For intrasexual competition and mate choice to occur within the same sex is thought to be quite rare in nature, and is not predicted by classical sexual selection theory. In cases where sex role reversals have been observed, males provide parental care or nuptual gifts, but there is no evidence for either in T. tetraophthalmus (McCauley and Reilly, 1984; Lawrence, 1986). Price and Willson (1976) found that the number of ovarioles and egg size are positively correlated with female body size in this species. Thus, in females, body size may be correlated to fitness. It is generally believed that female body size is related to fecundity in a very broad variety of insects. Lawrence (1986) suggested that because the local sex ratio can vary during the duration of a single copulation in T. tetraophthalmus, males should benefit most by choosing the most fecund females in female-biased situations, while displaying male-male competition for access to such females in male-biased situations.

Lawrence (1986) showed that sex ratios in the milkweed beetle can vary rapidly within and between patches of milkweed, and that this form of variation can have pronounced effects on male behaviors and on the structure of the mating system. Although Lawrence did not measure sexual selection on his beetles, it would seem likely that

the sex ratio variations he observed would favour large male body size (fighting ability) in male-biased situations and traits facilitating choosiness and the ability to choose in female-biased situations.

Lawrence (1987) also tested the predictions that smaller male T. tetraophthalmus beetles should disperse from milkweed patches with male-biased sex ratios (an alternative mating tactic conditional on male body size and local sex ratio), and remain in patches with female-biased sex ratios more readily than larger males, and field data substantiated these predictions. Small males were more likely to disperse from patches with male-biased sex ratios and were more likely remain in patches with female-biased sex ratios than were larger males.

Shelly and Bailey (1992) examined mate choice by males of an undescribed katydid species of the subfamily Zaprochilinae in relation to prior encounter rate with females. The spermatophore in this species represents about 16% of male body weight and a 5 day recovery period is required before males can remate. Therefore males incur substantial costs by mating. Two experiments were performed. In experiment 1, female encounter rate was manipulated in the laboratory where singing males, collected at random from the field were given either frequent contact or no contact with females. In experiment 2, singing males were taken from naturally occurring female-rich (female: male ratio 1.10 to 0.96) and from female-poor (0.55 to 0.50) areas. It was assumed that males from female-rich areas had more frequent contact with females than males from female-poor areas. Mating trials were conducted identically for both experiments. Males from all treatments were presented to single

different sized females and then compared with respect to their mate size selectivity. Males were not presented simultaneously with two females (large and small) because it was thought that zaprochiline males encounter females sequentially: simultaneous approach by two females to a calling male is a rare event (Simmons and Bailey, 1990). In both experiments, males with previous low-female encounter rates were more likely to mate than males with previous high-female encounter rates. The decreased mating activity of high encounter rate males resulted from a tendency to reject lighter (less fecund) females. This study demonstrated that female encounter rate, a consequence of local sex ratio, influenced mate choice by zaprochiline males. The two sexes appear to have spatial distributions that are independent of each other. Females aggregate in rich food patches such as kangaroo paw flowers, while males maintain a somewhat uniform distribution. Spatial differences in the adult sex ratio can therefore be quite pronounced in a system such as this. Why males do not settle in areas of high kangaroo paw density, where females are abundant, and where they can practice mate choice to maximize their reproductive potential, is not clearly understood.

Wilson's phalarope, Phalaropus tricolor, is a sex-role reversed, non-territorial shorebird. Some females are able to obtain more than one mate and the males provide nearly all of the parental care. Thus, female phalaropes, rather than males, should experience stronger intrasexual selection. Colwell and Oring (1988) examined the relationship between the operational sex ratio and female-female competition for mates, the prediction being that increasingly female

biased sex ratios should result in higher levels of intrasexual competition. Sex ratios in P. tricolor are generally female biased. Naturally occurring sex ratio variation was utilized in this study. Females arrive first at the breeding ground, so that sex ratios were more strongly female biased early in the breeding season. Seasonal changes in the availability of males for females resulted from interaction between parental care and female emancipation, as well as the asynchronous spring arrival schedules of the sexes, and clutch failure resulting in renesting opportunities. Colwell and Oring measured intrasexual competition as courtship chases, percent males defended, rate and intensity of mate defense and female-male proximity. These measures varied significantly among and between years. Using univariate and multivariate correlations it was shown that the strength of the predicted relationship between sex ratio and measures of intrasexual competition also varied among years. However, there was a general agreement between sex ratio and measures of intrasexual competition, indicating that the operational sex ratio may provide a useful estimate of the opportunity for sexual selection.

Although Colwell and Oring (1988) showed that the operational sex ratio can affect behavior associated with reproduction in Wilson's phalarope, they approached the sex ratio question from a different perspective than most of the previous studies reviewed here. First of all, Colwell and Oring did not manipulate sex ratios, they used natural variation, and second they asked whether sex ratio is a good indicator for the strength of sexual selection. They concluded by stating that it is, but they did not actually measure sexual selection,

they assumed that the strength of sexual selection is correlated to levels of intrasexual competition. The operational sex ratio, was proposed by Emlen and Oring (1977) as an empirical measure of sexual selection which often may be correlated with levels of intrasexual competition, but they go on to say that it (intrasexual competition) is neither a necessary nor sufficient condition for sexual selection. To conclude that the operational sex ratio is a good indicator of the strength of sexual selection in P. tricolor because of this correlation (with no evidence for it in this species) may be premature.

Acoustic Communication, Sexual Behavior and Selection in Crickets and their Relatives

This section begins with reviews on the physical and genetic basis for the production and reception of calling song. The calling songs of male field crickets (Orthoptera: Gryllidae) are species specific and function to attract sexually receptive females, repel other calling males, and act as cues for terminating migratory flights of conspecifics (Alexander, 1957a; Alexander, 1957b; Campbell and Shipp, 1979; Cade, 1989). Various aspects and consequences of calling behavior are discussed, with emphasis on their significance to the mating system. This section concludes with reviews of aggressive behavior, courtship and mating in the Gryllidae.

Mechanisms of Song Production

The pulse, the fundamental element of gryllid calling song, is produced by rubbing the tegmina, modified front wings, together in a characteristic scissoring motion, termed stridulation. Each tegmen has integrated within it modified veins which act as a scraper (the

plectrum) and a file (the pars stridens). However, only one of each is used to stridulate, usually right tegmen over the left. The plectrum-pars stridens impact set up a series of vibrations which are then amplified by another specialized structure of the tegmen, the harp. Each convergent stroke of the tegmina produces a single pulse, while divergent strokes are silent. Pulses are organized into species-specific temporal patterns. Two general types of song can easily be distinguished in field crickets. When pulse trains are relatively short, as in G. pennsylvanicus, the song is termed a chirping-type song. In other species, such as G. integer and G. rubens, pulse trains are considerably longer and this type of calling song is termed a trilling song. There exists a one-to-one relationship between arriving nerve action potentials, contraction of muscles (medial dorsoventral muscles responsible for the convergent stroke, basalars and subalars responsible for the divergent stroke) and pulses (Pringle, 1957). It is hypothesized that a central pattern generator for calling song resides within the thoracic ganglia, but this remains to be characterized (Kutsch and Huber, 1989). Sensory input arriving from the brain is also important in determining the individual's calling behavior. Song modification may occur through various sensory feedback mechanisms activated by cues from the physical and social environments. Since the neural network required to produce complete calling song resides within the thoracic ganglia (Kutsch and Otto, 1972), sensory input and sensory feedback from other ganglia serve to initiate, modify and terminate calling behavior.

Souroukis et al. (1992) found that the calling songs of laboratory reared G. integer did not change in response to age.

Furthermore weight at eclosion and flight wing length was not related to song structure. However, some environmental factors such as temperature and the time of calling, had significant effects on a number of song parameters (see also Walker, 1962; Walker, 1974; Sakaluk and Sneddon, 1990). A number of studies have documented circadian control of singing as well as a number of other activities in Gryllus (Wiedenmann and Loher, 1984; Honegger, 1981).

Mechanisms of Sound Reception

Sound reception in gryllids is relatively complex involving several organs; the tympanal organs, the subgenual organs, the tracheal organ system (Young and Ball, 1974) and filiform hair sensilla (Ball et al., 1989). The tympanal organs, located on the anterior and posterior sides of the forelegs near the proximal ends of the tibiae, contain at least two types of auditory receptor cells. One type is sensitive at a narrow frequency range of about 4.5-5.0 KHz, corresponding to male calling song carrier frequency. Recognition of calling song occurs in the prothoracic ganglion and perhaps in the brain (Schildberger et al., 1989). The other type of auditory receptor cell has a far greater range extending from about 3.0-40.0 KHz. Since many species of crickets are nocturnal fliers, echolocating bats are potential predators. The ability to pick out high frequency signals may be an important capacity with respect to bats. A number of nocturnal flying insects have evolved tympana with the ability to hear the ultrasonic signals of bats (reviewed by Pollack and Hoy, 1989). Trigonidiun cicindeloides is a songless species in which only the long winged forms, those exposed to nocturnal echolocating bats, develop tympana (Walker and Masaki, 1989).

The subgenual organs are found in all 6 tibiae and are important in the detection of substrate vibrations. The filiform hair sensilla on the cerci are capable of detecting a range of sound and are individually innervated by one sensory cell, the dendrite of which is coupled to the base of the hair (Elsner and Popov, 1978). The length of these hairs varies from 0.1-1.6 mm. The longer the hair, the greater its sensitivity at low frequencies and the narrower its effective frequency range. Sensilla of varying lengths, along with differential sensitivities of receptors have produced a system able to perceive intensity and direction, over a wide range of frequencies (Elsner and Popov, 1978).

Genetics of Cricket Acoustic Behavior

The study of the inheritance of song characteristics in crickets has a long history. As early as 1933, Fulton produced hybrid crosses of Nemobius fasciatus and N. tinnulus, to investigate the genetic basis of cricket song. The hybrid males sang intermediate song types, which led Fulton to conclude that 2 or more "determinators" of song were segregating. Bigelow (1960) used hybrids obtained from crossing G. rubens with G. veletis and with Acheta assimilis (possibly G. pennsylvanicus). He concluded that certain features of the hybrid male's songs were intermediate, while other features resembled one or the other of the parental species. Bentley and Hoy (1972) made extensive measurements of hybrid song characteristics using Teleogryllus commodus crossed with T. oceanicus, and G. armatus crossed with G. rubens. From this work they drew three important conclusions: (1) since some song parameters are sex-linked while others are not, more than one chromosome is involved in the system;

(2) the presence of sex-linked and non-sex-linked parameters demonstrates that different sets of genes are involved in the control of different operations of the neural network; and (3) since the sex-linkage observed is not complete, these genes are influenced by other genes on other chromosomes.

Another set of characteristics of the calling song deal with time and energy investment on a broader scale, and this includes the characters nightly calling duration and calling bout duration. Cade (1981) showed that considerable genetic variation exists among G. integer males with respect to the amount of time spent calling each night. Artificial selection experiments demonstrated that the mean nightly calling duration of G. integer was under genetic control, with heritabilities of about 0.5. More recently, Hedrick (1988) showed that calling bout length in G. integer was heritable (h^2=0.75).

A number of studies have investigated the genetic relationship between sender and receiver in gryllid acoustic communication. When hybrid male crickets produce intermediate song types, the hybrid females show preference for these hybrid songs over the parental songs (Hoy and Paul, 1973; Hoy, 1974). Huber (1962) suggested that the genetic differences that cause variations in song, perhaps even the particular difference in the structure of the central nervous system itself, are exactly the same as the differences which cause the variations in response. Alexander (1962) first proposed that a genetic "linkage" between male song and female preference would ensure that they remained correlated during periods of evolutionary change, thus making the system more persistent and robust. Hybrid females of Teleogryllus commodus crossed with T.

oceanicus were significantly more attracted to hybrid song than either of the parental stock songs (Hoy and Paul, 1973) and this was proposed as being evidence for genetic coupling. Ritchie (1992) investigated genetic coupling in the tettigoniids, and provided more evidence for such genetic coupling. Hybrid females from song races of the bushcricket, Ephippiger ephippiger, showed clear preference for hybrid male songs. In contrast, female T. oceanicus recognized calling song after the interpulse interval sequence had been randomized, an observation that did not support the genetic coupling hypothesis. Furthermore, studies of crosses between pairs of grasshopper species did not support the genetic coupling hypothesis (reviewed by Elsner and Popov, 1978). Doherty and Hoy (1985) proposed a coevolutionary hypothesis. Coevolution does not require similar mechanisms between sender and receiver. Two distinct mechanisms that operate together over evolutionary time would become efficient due to the selection acting on them. They suggested that genetically independent but coevolved caller-reciever mechanisms could be selected for so that individuals could produce and respond to the appropriate calls. Furthermore, Butlin and Ritchie (1989) emphasized that hybrid behavioral coupling does not provide particularly good evidence of genetic coupling because if separate genes controlling differences between the species act additively, then hybrids should show intermediate songs and preferences. The genetic coupling hypothesis, as proposed by Alexander (1962), is an important concept because it could be applied to a much wider range of communication systems. Whether genetic coupling or coevolution applies to cricket communication systems remains to be resolved.

Sources of Selection on Acoustic Behavior

Male gryllids require about 1 week after eclosion for their gonads to mature and thus to produce their first spermatophore. For example, within one week of eclosion, male G. pennsylvanicus begin producing their species-specific calling song (Cade and Wyatt, 1984), at which time they announce their sexual status. In this section the various modes of selection on calling song will be discussed. These include female attraction and female choice, male-male competition, predation and parasitism, and environmental factors.

The calling songs of field crickets serve primarily to attract potential conspecific mates. Natural selection, through the pressures of predation and parasitism, should select for an inconspicuous song, while sexual selection should favour a more conspicuous song easily discernible to females. The calling songs of field crickets can be broken down into several, continuously varying "song parameters". These characteristics of the calling song however may not be very important to female choice. Calling song may simply function as a long distance congeneric attractor. Having found a male, a female may choose to mate or not based on courtship performance or other short distance cues. Whether or not female choice really operates on calling song is not precisely known. Currently, the three competing hypotheses for the evolution of female mating preferences are Fisherian runaway sexual selection, the good genes hypothesis and sensory exploitation. The first two hypotheses predict that characters and preferences coevolve, whereas the sensory exploitation hypothesis predicts that male traits evolve to exploit preexisting female biases. The good genes hypothesis states that a conspicuous

caller would demonstrate his energy reserve, his health, his ability to foil predators, and/or the quality of the burrow he has defended (Ryan and Keddy-Hector, 1992). All these factors should be important to females. Besides, Hedrick (1986) who found that females preferred longer calling bouts in Californian G. integer, not much work has been done in this area. Since calling song requires a great deal of energy (Prestwich and Walker, 1981), a more energetic song could indicate a successful healthy male. Hedrick's findings may support this hypothesis because calling bout length might be directly proportional to energy invested.

The other important function of calling song is intrasexual competition. Male G. integer have adopted two tactics for meeting females: they call or they search silently in the vicinity of a calling male (Cade, 1979a; Cade, 1981). Most males of this species call to attract mates. However, a proportion of males (termed satellite males) may adopt alternative mating tactics. These satellites usually do not defend territories. They will, instead, search and position themselves so as to intercept females attracted to a calling male (Cade, 1979a; Cade, 1984). The proportion of time that males spend in each of these tactics appears to depend on population density (French and Cade, 1989; Cade and Cade, 1992). It may also depend on a number of other factors such as the operational sex ratio. Cade and Cade (1992) found a significant negative correlation between calling and searching at low population density, but not at high density in G. integer. These male mating tactics are discrete, but conditional. Therefore, it is appropriate to treat these male reproductive tactics

as being continuously distributed traits when considering the entire lifetime of individuals (Cade, 1984).

Otte (1977) suggested that the costs associated with calling may, under certain circumstances, outweigh the benefits. Therefore selection may favour such a genetically determined calling-male versus silent-male dimorphism. Campbell and Clarke (1971) showed that calling males of T. commodus were not randomly distributed in a field. Furthermore, Campbell and Shipp (1979) found that males tended to move away from a close loudspeaker playing conspecific song, but towards a distant loudspeaker. Heiligenberg (1966) discovered that the chirp rate of a territorial male A. domesticus could be increased by playing calling song through a nearby tape recorder. Souroukis et al. (1992) found that the intertrill interval of G. integer was significantly less in the field than in acoustically isolated laboratory males. It appears that male field crickets are able to vary their behavior in response to the degree of acoustic competition they encounter. In low to moderate density situations, it is likely that intrasexual competition, mediated through calling song, is primarily responsible for the distribution of males in a field. At higher densities, aggressive interactions should become more frequent, and thus should play a larger role in determining male spacing patterns.

The males of some species of acoustic Orthoptera participate in what have been termed choruses and leks (see Alexander, 1975 and Otte, 1977). Periodical cicadas, honeybees, Melanesian fireflies and some Hawaiian fruitflies, are examples of other insects which show lek-breeding behavior. Male katydids, Orchelimun vulgare, aggregate

and call in the vicinity of female oviposition sites - particular plant stems (reviewed by Alexander, 1975). According to the classical definition, this should not be termed a lek because the aggregation does not form for the sole purpose of mating. Alexander (1975) suggested that resource-based mating aggregations should be included in the concept of the lek because intense sexual selection by females may be involved. In Orthoptera, aggregations with no function other than mating have been difficult to identify. In many species of field crickets, including G. integer and G. pennsylvanicus, males sometimes form choruses. These aggregations may form around high quality burrows, therefore they may be termed resource-based leks. Field cricket aggregations resemble leks in some important ways: (1) displaying males are in close proximity, (2) males adopting satellite tactics are frequently associated with these aggregations, (3) females are attracted and mate within these aggregations (Cade, 1979a).

The factors leading to the development of such lek-breeding behavior are the subject of much debate (Bradbury, 1981). Female choice, female distribution and mobility, and predation have been considered as possible reasons for the evolution of lekking behavior. Lack (1968) wrote that communal leks have evolved 9 times in birds. When all other extant groups that show lek-breeding behavior are considered, this figure will grow considerably. Many characteristics of leks however, appear to be conserved across a wide range of animals. Therefore, there may be a few universal factors responsible for the evolution of lek-breeding behavior. Otte (1977) suggested several possible benefits of lek formation in acoustic

Orthoptera. A chorus could attract more females because: (1) it would have a greater area of influence from which to attract randomly wandering females; and (2) it would cast a larger acoustic shadow, reducing the chances of a nearby single calling male being found.

Calling song has been shown to attract a variety of predators, and the parasitic tachinid fly, Ormina ochracea (formerly Euphasiopteryx), in some species. Gravid females of O. ochracea can locate calling male G. integer and larviposit on or near them. The larvae then burrow through the exoskeleton and consume the host from inside. Once a male is infested with larvae, its nightly calling duration decreases gradually until death (about one week). Females and non calling males are rarely parasitized. Therefore males may be under selective pressure with respect to calling behavior (Cade, 1975; 1984).

Walker (1979) set a calling male, Anurogryllus arboreus over a pitfall trap, to determine potential predators. He found wolf spiders, katydids and spadefoot toads in his traps. The list of gryllid predators is probably quite extensive. Sakaluk and Belwood (1984) described how insectivorous Mediterranean house geckos, Hemidactylus tursicus, respond phonotactically to male Gryllodes supplicans and wait outside the burrows and intercept approaching females. Superficially, one would predict that sex biased predation in acoustic insects would work against males, but this study clearly illustrates how sex biased predation can operate in the direction that would not normally be predicted.

Another important source of selection in the evolution of cricket calling song is the physical acoustic environment. The songs of

particular species should have evolved for efficient transmission though the various acoustic habitats they occupy. Sound waves of particular frequency will behave differently in various environments. Vegetation can reflect and absorb sound, therefore the height and density of vegetation in the habitat should be important factors. Song should also have evolved to minimize interference introduced by the acoustic environment; background noise in the form of other Orthoptera, birds, wind, etc. (Bailey, 1990).

Aggression

During aggressive male-male interactions a characteristic aggressive song is produced. When two Gryllus conspecifics first come in contact the initial response is similar regardless of sex; they touch each other, primarily with their antennae. The ensuing behavior ranges from no reaction to aggression or courtship. Sex recognition, in a variety of field crickets, is facilitated by recognition of close range odors and contact chemoreception (Otte and Cade, 1976; Paul, 1976; Rence and Loher, 1977).

Alexander (1961) noted that when a group of males was placed in an enclosure, a dominance hierarchy was soon set up. Aggressive interactions ranged from warning chirps to lunges to overt physical interactions. When two males came into first contact an aggressive encounter usually occurred. In G. campestris, males are known to sing during the daylight hours, if a calling male senses a conspecific approach his burrow, he emits a warning chirp. The incoming male then flees or lunges forward to attack. In addition to stridulation, aggressive interactions often escalate to overt physical confrontations, where mandibles lock, opponents get thrown and in

some cases loose parts of limbs, wing covers and antennae. Field crickets engage in one of the more violent forms of male-male competition found anywhere. These fights may last from just a few seconds to several minutes (Alexander, 1961 and personal observations).

Dixon and Cade (1986) investigated factors that influenced aggression as well as the outcome of male-male encounters. Larger males generally won fights. They found that time of day and age after sexual maturity had no effect on measures of aggression. Winners were easily identified because they generally were more eager to reinstate physical contact, did not retreat and usually called afterwards. They found that the level of aggression was not related to the time of day. Pre-reproductive adult males (had not produced their first spermatophore) were not as aggressive as sexually active males, but age after sexual maturity had no effect on aggression. Furthermore, repeated trials using pairs of similarly matched males indicated that one male maintains constant dominance by winning most or all of the fights.

Courtship

Courtship in field crickets generally involves a characteristic courtship song and a variety of tactile and movement behaviors. Courtship behavior is usually highly stereotypic and follows a general pattern in most gryllidae.

Alexander and Otte (1967) showed that courtship and mating seemed to be identical in Gryllus and Acheta. They gave an account of the courtship sequence leading to copulation. Males and females usually antennate each other upon initial contact then the male

slowly turns his body away while stridulating, a mixture of calling and courtship songs, and rocks his body gently from side to side. After turning away, the male continually reaches back toward the female with his hind legs and antennae and backs toward her. When the female antennates and palpates the rear of the courting male, he stops courtship stridulation, flattens his tegmina against his body, and backs up, extending his abdomen under her, while whipping his antennae back over his body and against the female. The female mounts by moving forward over the male's flattened body.

The courtship song of most gryllids is quite different from the calling song or aggressive stridulation. Courtship song is still generated by the tegmina, but the resonant frequency of the harps is probably altered. Alexander and Otte (1967) stated that much of courtship stridulation might be the result of the tegmina striking the sides of the abdomen because the tegmina are held at a much lower angle during the courtship song. The presence of courtship song during the courtship ritual of A. domesticus, appears to be important. Males who had their tegmina removed, and thus unable to produce courtship song, were not mounted by females. However when females were presented to these males while courtship song was broadcast over a loudspeaker, the female mounted the male in each case and 62% of these mountings resulted in successful matings (Crankshaw, 1979).

Copulation, Sperm Competition and Oviposition

Many aspects of copulatory and post-copulatory behavior are species specific in field crickets, the following account is somewhat generalized for Gryllus. When genital contact is made a

spermatophore is transferred. This process may take up to 30 seconds, during which time the pair remain motionless. A few seconds after the spermatophore is attached the female dismounts and the male immediately begins post-copulatory guarding behavior. He maintains contact by continually antennating her and is aggressive toward other males. The male may even produce calling song at this time, while the female remains relatively immobile. During this time, which may last for about an hour, the male forms another spermatophore and may remate with the same female. Eventually the female removes the spermatophore by dragging her abdomen on the ground or by reaching back with her mandibles and dislodging it (Alexander and Otte, 1967; personal observations particular to G. pennsylvanicus).

The Gryllus spermatophore is relatively small and comparatively inexpensive for males to produce. In contrast some male Tettigoniids such as Anaborus simplex, the mormon cricket, produce large nutritious spermatophylaxes which are passed to the female with the spermatophore. This form of male parental investment is substantial. In the mormon crickets the spermatophore/spermatophylax complex approaches 20% of the male's body weight. Furthermore, the male requires several days to produce another. The spermatophylax nutrients are known to affect female fecundity and the size of eggs, and females may gain nutritional benefits by exercising multiple mating (Gwynne, 1984). These factors have profound consequences on the structure of the mating system. In several Tettigoniid species, complete sex-role reversal has been observed, where males choose mates and females

compete among themselves for mating opportunities (reviewed by Gwynne, 1991; Simmons, 1992). Biased operational sex ratios may also result in these systems as food quality varies (Gwynne, 1990; see review in previous section).

Sperm competition and patterns of sperm precedence, the sequence in which the sperm from different mates is utilized and the proportion of total eggs fertilized by each ejaculate, have important implications for reproductive behavior and the structure of the mating system. Sperm competition can lead to opposing selective forces: selection on males to pre-empt sperm from previous matings, such as, sperm removal in many Odonata (Waage, 1979) and in the tree cricket, Truljalia hibinonis (Ono et al., 1989), and selection on males to prevent further insemination of their mates, such as, post-copulatory mate guarding. Few sperm utilization patterns have been determined among the Gryllidae. Sakaluk (1986) examined such patterns in doubly-mated females of Gryllodes supplicans, and found that the first male to mate had a small advantage, fertilizing about 60% of the offspring produced. Sperm competition was also examined in G. integer using doubly-mated females. The results suggested that there was a second male advantage with about 72% of the eggs being fertilized by the second male (Backus and Cade, 1986). However, it was concluded that a large amount of sperm mixing occurs. The different patterns of sperm precedence between G. supplicans and G. integer, may reflect differences in spermathecal shape. Walker (1980) suggested that species having spermathecae that were spherical tend to favour the first male to mate, whereas elongate or tubular spermathecae should result in second or last male

precedence. The shape of spermathecae of G. supplicans becomes more oval with repeated matings (Sakaluk, 1986), whereas that of G. integer is spheroid and only slightly elongated (Backus and Cade, 1986). A yet to be quantified amount of intraspecific variation occurs in the shape of these organs in G. integer following mating (Murray pers. comm.; personal observation). Simmons (1987b) showed that sperm mixing also occurs in G. bimaculatus.

The ovipositor of female field crickets is long, slender with a sharp, lance shaped tip, composed of two pairs of parallel valvulae. The outside of all four valvulae is covered with hair sensilla able to detect suitable substrate for egg laying. This structure is very similar to that of most other soil-laying Gryllidae. Field cricket oviposition behavior in nature is poorly understood, especially with respect to: frequency, age and mated status. An apparently overlooked aspect of field cricket sperm competition concerns the timing of egg release by females. The status and distribution of male ejaculates at the time when an egg passes by the aperture of the spermathecal duct, should be crucial in determining paternity. Egg release is triggered hormonally in field crickets. In T. commodus insemination triggers the release of eggs within the next 12-24 hours (Loher and Dambach, 1989). The control and choice that females are able to exercise over the release of eggs, or even mating decisions at the onset of egg release, could have a significant affect on the paternity of subsequent eggs. It would be interesting to examine spatial and temporal aspects of mating and oviposition in nature. In the laboratory, female field crickets can lay 350-650 eggs during their lifetime (Cade and Tyshenko, 1990). The stimulus for egg-laying appears to be a

combination of substrate moisture and consistency. Eggs are pushed through the ovipositor by rhythmically alternating movements of the valvulae and deposited singly at intervals of 10-20 seconds. Eggs are usually deposited in several tightly clustered groups of 3-7 (Loher and Dambach, 1989). No more parental investment is usually involved.

The Study Animals

Gryllus pennsylvanicus is commonly known as the northern fall field cricket, and ranges widely across the north-eastern part of North America, from the eastern seaboard south to North Carolina and west into Kansas. The northern limits are poorly known, but it is not believed to extend into the Canadian shield. There are also reports of G. pennsylvanicus out on the west coast, in Washington, Oregon and southwestern British Columbia (Alexander, 1968).

Gryllus pennsylvanicus is univoltine and overwinters in the egg stage. Hatching occurs in early spring and over the next few months the nymphs undergo between 5-7 molts (Alexander, 1968; Masaki and Walker, 1987). In the Niagara peninsula, G. pennsylvanicus reaches adulthood in late July and can be found in the field until the first frosts (late October, sometimes into November). These adults mate, oviposit and the eggs produced by this generation overwinter. G. pennsylvanicus lives in old field and short grass habitats. Both nymphs and adults seem to occupy the same ecological niche.

Flight wing dimorphism occurs in many field crickets with only macropterous individuals being capable of flight dispersal and shows significant between-season and within-season temporal and spatial variation in the proportion of macropterous (long-winged)

individuals (Harrison, 1979; Walker and Sivinsi, 1986). Zera and Rankin (1989) have shown a significant genetic component to morph determination in G. rubens. The frequency of long-winged G. pennsylvanicus is quite low (range 0-13%) compared to some other North American field crickets.

The cricket song commonly heard by humans at night is calling song. When pulse trains of calling song are relatively short, such as in G. pennsylvanicus, the song is termed a chirping-type song. As is the case with most field crickets, G. pennsylvanicus males produce another type of song during aggressive interactions, the characteristic aggressive song. It is similar to the calling song in the respect that pulses are practically indistinguishable. The primary difference however, is in the length of the pulse trains, which are generally longer (often >10 as compared to 3 or 4 in calling song) and much more variable in length, within a single song. Also, the intensity of aggressive song (which can exceed that of calling song) often fluctuates as compared to the constant intensity of calling song. One or both males may stridulate during aggressive interactions (Alexander, 1961; personal observations).

The third type of song, courtship song, has a carrier frequency of 5.5-6.0 KHz in G. pennsylvanicus as compared to 5.0 KHz for calling song. The intensity of courtship song is also much lower in this species than the 90 dB level sometimes achieved during calling, and the pulses (as they appear on a sonogram) blend together more, as if sound was being generated during both convergent and divergent strokes of the wing covers. What appears to be the pulse trains of the courtship song, are fairly invariant in length, and intermediate in

length between those of calling and aggressive stridulation. A striking feature of courtship song are the characteristic "tick" sounds which are interspersed regularly between the soft courtship pulses (Alexander, 1967; personal observations).

Average adult life expectancy in nature probably ranges from 1-4 weeks, however field captured adults have been kept alive in the laboratory for up to 8 weeks (personal observation). Gryllids are omnivorous. Gangwire (1961) described their diet as consisting of plant tissue, livestock manure, other feces, dead vertebrates, mantid eggs, and various live invertebrates (especially termites). G. pennsylvanicus is also a major predator on apple maggot pupae and a variety of other pupae buried 1-3 cm in soil (Monteith, 1971).

METHODS

This entire experiment was performed on the campus of Brock University, St. Catharines, Ontario, Canada, during August and September, of 1990 and 1991. One large outdoor enclosure (arena) served as the study area.

Experimental Design

The 4 sex ratios investigated (in males to females) are 5:0, 5:2, 5:5 and 5:10. Sex ratio was manipulated by adjusting the number of females in the arena. Male density (n=5) was always kept constant throughout the experiment. All individuals used in subsequent analyses were observed for 30 hours or 3 nights. When observations were not being conducted (daytime or postponed nights due to weather), all individuals of that replicate remained in the arena until the replicate was completed. The minimum amount of time a replicate of crickets could spend in the arena was 72 hours (14 h acclimation period + 10 h observations [night 1] + 14 h [day 1] +10 h observations [night 2] + 14 h [day 2] + 10 h observations [night 3]), this ranged up to over 170 hours per replicate of crickets, dependent on the weather. In the event of a death (3 occurrences out of 175 individuals sampled), an unmarked individual was released into the arena to restore the sex ratio. The dead individual and its replacement were not used in the analysis, however, the remaining individuals within that replicate were utilized. Using data from French and Cade (1989) it was calculated that a sample size of $n \approx 24$ was sufficient to estimate mean male mating success to 0.1 at the 0.05 level of significance. Thus the study was designed to consist of 5

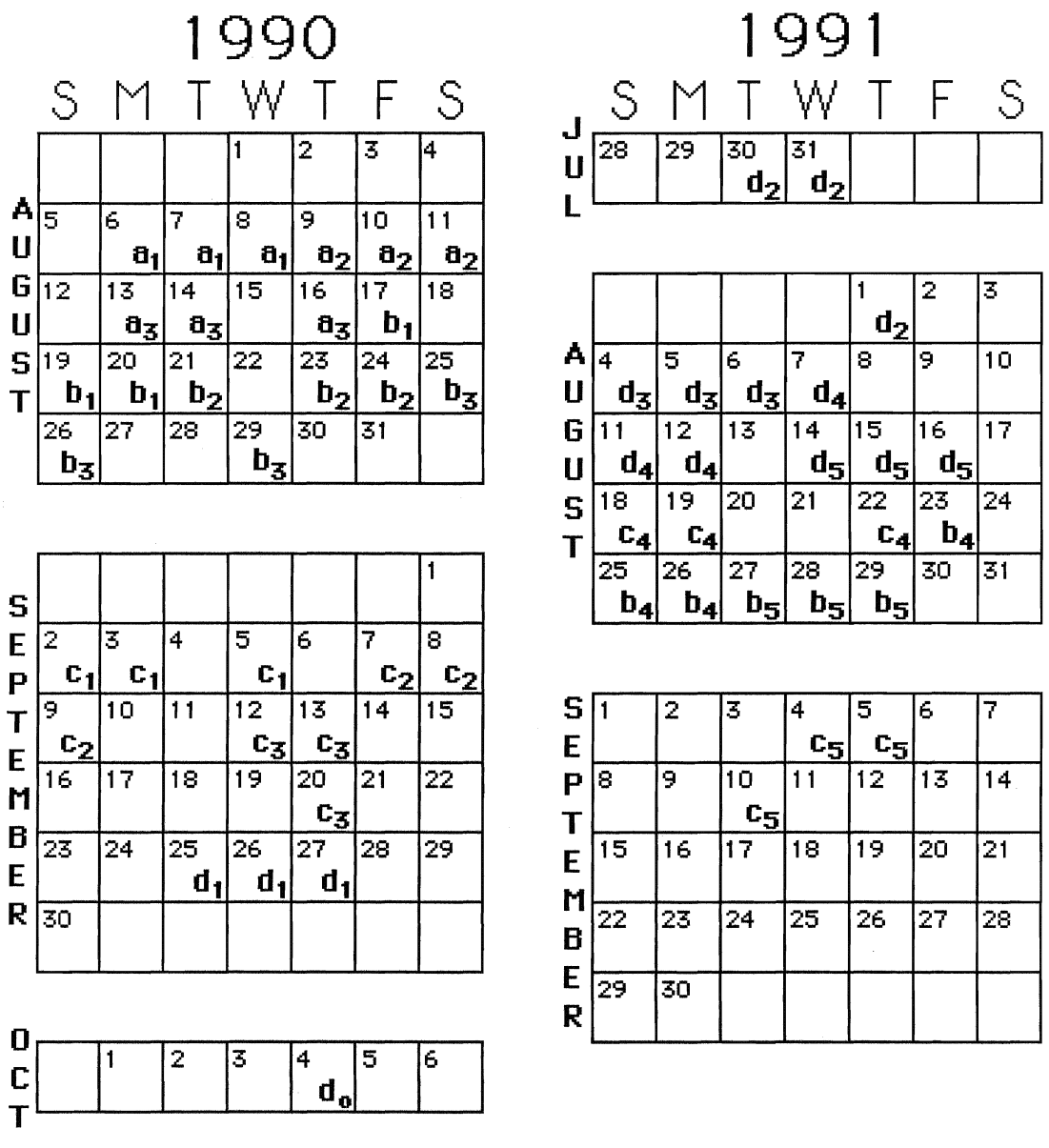
replicates at the 5:2, 5:5 and 5:10 sex ratios, while fewer could be performed at 5:0 (see Figure 1. for schedule of data collection).

Several criteria were used to control for the natural variation in weather that could have contributed to variation in behavior between replicates, years and sex ratios. These include (1) temperature, no upper limit was set, but nights where the minimum approached 10° C were avoided. (2) Precipitation, if substantial probability for prolonged periods of rain existed observations were postponed. (3) Wind velocity, high wind velocity (frequent gusts of >25 kts) caused the aluminum walls of the arena to rattle, and also made it difficult to hear courtship song, these nights were also avoided. These criteria were employed in an attempt to homogenize meteorological conditions.

Outdoor Arena

The arena used in this study is located on a second story balcony, in the science complex at Brock University. It was built on a well drained patio stone floor. The arena measures 9.6 m long by 4.3 m wide. It was framed using pressure treated 6.5 cm by 3.5 cm planks, which were then covered by flat aluminum sheets. The walls are 0.92 m high. Along the bottom inside edge, 10 cm aluminum angle was used as a seal. Aluminized duct tape was then applied over all holes and seams, and the entire bottom surface was covered in 5 cm of medium grain sand; this made the arena "cricket-proof". The arena was divided into 36, 1.1 m by 1.1 m quadrats. The quadrats were numbered and their corners were marked on the aluminum walls and by red wooden pegs anchored into the substratum.

Figure 1. Distribution of data collection over two field seasons. Lower case letters (a, b, c and d) refer to the four sex ratios investigated in this study: 5:0, 5:5, 5:10 and 5:2, respectively. Subscripts indicate replicate number. In total, 55 nights of observations were conducted. The replicate initiated Oct. 4, 1990 was not completed, and these data are not included in the analysis.


1990
S M T W T F S
AUGUST
5 6 a1 7 a1 8 a1 9 a2 10 a2 11 a2
12 13 a3 14 a3 15 16 a3 17 b1 18
19 b1 20 b1 21 b2 22 23 b2 24 b2 25 b3
26 b3 27 28 29 b3 30 31
SEPTEMBER
1
2 c1 3 c1 4 5 c1 6 7 c2 8 c2
9 c2 10 11 12 c3 13 c3 14 15
16 17 18 19 20 c3 21 22
23 24 25 d1 26 d1 27 d1 28 29
30
OCT
1 2 3 4 do 5 6
1991
S M T W T F S
JUL
28 29 30 d2 31 d2
AUGUST
1 d2 2 3
4 d3 5 d3 6 d3 7 d4 8 9 10
11 d4 12 d4 13 14 d5 15 d5 16 d5 17
18 c4 19 c4 20 21 22 c4 23 b4 24
25 b4 26 b4 27 b5 28 b5 29 b5 30 31
SEPTEMBER
1 2 3 4 c5 5 c5 6 7
8 9 10 c5 11 12 13 14
15 16 17 18 19 20 21
22 23 24 25 26 27 28
29 30

Artificial shelters were provided for refuge and for calling sites (males prefer to call from sheltered sites). Shelters were placed on the sand at the center of all quadrats and for quadrats adjoining the walls, they were also positioned midpoint against the wall, so that a total of 62 shelters were deployed. The shelters themselves were constructed of 2 cm thick plywood and measure 16 cm by 11.5 cm by 3.5 cm high (interior dimensions). To protect the crickets when observations were not being conducted, three overlapping sections of 1 cm nylon orchard netting that were fixed to one long side of the arena could be stretched across the top. The netting was used primarily to keep birds out, but also proved effective against squirrels and chipmunks. Food and water was supplied ad libitum, in the form of a hand held sprinkler, cat food pellets and naturally occurring dead arthropods.

Collecting and Culturing

All individuals used for this experiment were collected as last instar nymphs (≈75%) and as adults (≈25%), in St. Catharines and the surrounding area. All crickets were cultured indoors up to the time they were to be observed. Males and nymphs were kept in a large indoor enclosure (3 m x 3 m), similar in construction to the much larger outdoor arena. This enclosure was checked every few days for newly eclosed females, which were removed and placed in the all female culture. The female culture was a 50 gallon terrarium, with a sand bottom and ample shelter in the form of egg cartons. Cat food pellets and water was again provided ad libitum in these cultures.

Both cultures were located in the same room. Light was provided in the form of ceiling mounted fluorescent lights and four

heat lamps 1 m off the surface of the sand. The light-dark cycle was maintained at 14:10 hours (late summer at this latitude) and synchronized with outdoors. Both sets of lights were on separate timers, so that half an hour dawn and dusk periods were incorporated (fluorescent lights on, heat lamps off). An air conditioner was kept on the "low" setting which corresponded to about 30% relative humidity. About 14 hours prior to the start of observations a new replicate of crickets was picked at random. Weight was measured once, to the nearest milligram using a Mettler BB240 electronic scale, approximately 14 hours before the start of behavioral observations. Those crickets were then individually marked using Testors Enamel ® (commonly known as model airplane paint), and released into the center of the arena for the acclimation period.

Quantification of Behaviors

Scale maps of the arena (1:43) were constructed and used hourly to record data on searching/movement, calling, fighting, courtship and mating. Notes were also made for oviposition, feeding and air temperature. All individuals were located at least once every hour (complete arena checks) using a battery operated headlamp. Partial arena checks were carried out as needed, in order to identify individuals performing particular behaviors. Mated females were also checked more frequently to ascertain the condition of the spermatophore and to check for rematings.

Searching (for males) and movement (for females) was estimated as the sum of hourly displacements. The position of all individuals was recorded on a different map hourly. Displacement

was later extrapolated from these maps and reported in meters. This is an underestimate of actual mobility because straight-line paths are assumed. This measure of mobility however was significantly correlated with actual mobility in the northern spring field cricket, G. veletis (Souroukis and Cade, unpublished data), and thus provides an estimate which is proportional to actual mobility.

Calling was estimated as the sum of five minute sample intervals a particular male was heard calling for any duration. Each sample interval was scored as 5, thus the maximum possible score that could be achieved by a male during 30 hours of observation was 1800. This is an overestimate of actual calling duration (in minutes), but again would be proportional to actual calling duration.

Fighting was defined as any male-male encounter which escalated to aggressive stridulation. The winner was deemed to be the one who remained in the area and usually began to call (the loser retreated and/or did not call). This behavior was measured as frequency of occurrence.

Courtship was defined as any encounter between a male and a female which resulted in courtship stridulation. These encounters may have or may have not led to mating. Again, measured as frequency of occurrence.

Male mating success was defined as the total number of successfully attached spermatophores by a particular male. An improperly attached spermatophore did not qualify as a mating (occurred 5-10%). In cases where two or more males were under the same shelter with a mated female, the mated male could be inferred by guarding behavior. Although patterns of sperm precedence have

not been determined in this species, an assumption made for the purposes of this study is that all matings were equivalent.

Analysis of Data

Nonparametric tests (Mann-Whitney U-tests and Kruskal-Wallis one-way ANOVAs) were performed on raw data to detect significant differences between replicates and between field seasons for all distributions. About 4.5% of the 88 tests showed a difference at the 0.05 level of significance. This is approximately the proportion of significant results expected by chance alone. Therefore all data were pooled between replicates and between field seasons. All phenotypic characters were transformed using natural logarithms except % fights won which was transformed using the acrsin[x] function.

This research focused on three primary questions. (1) How does behavior change in response to sex ratio? (2) How does the opportunity for sexual selection respond to changes in sex ratio? And (3), how does selection operate at different sex ratios? To determine how behavior changes with sex ratio, one-way ANOVAs were performed on the transformed distributions of behavioral traits, to test for differences between means among all 4 sex ratios. If ANOVAs were significant, Scheffe'e F-tests for pairwise comparisons within model I ANOVAs were used to determine where the differences occurred.

To estimate the opportunity for sexual selection, male mating success data were reorganized according to replicates (not pooled) within the male-biased, unity and female-biased sex ratios. The opportunity for sexual selection (I = standardized variance of male

fitness), was calculated for each replicate. This technique produced 5 independent I-values for each of the 3 sex ratios, thus facilitating the use of a one-way ANOVA to test for a difference in the opportunity for sexual selection between sex ratios.

To measure the intensity of sexual selection at the various sex ratios, selection differentials and selection gradients were calculated for the phenotypic traits of weight, calling and searching. Transformed data were standardized to have sample means of 0 and standard deviations of 1. Relative male mating success was estimated by dividing each individual male's mating success by the mean male mating success within each sex ratio (Lande and Arnold 1983). The selection differential measures both the direct force of selection on a character as well as the indirect forces due to selection on correlated characters. It is estimated as the covariance (Lande and Arnold 1983) or as the univariate regression coefficient (Falconer 1981), between relative fitness and the character of interest. In this study, the univariate regression coefficient rather the covariance was used to estimate the selection differentials because this method allows standard errors to be assigned to the selection differentials so that they can be tested for significance just as any other regression coefficient. Furthermore this method facilitates better comparison between the selection differentials and the selection gradients (Conner 1988). Statistical significance of all selection differentials was determined using two-tailed t-tests.

The selection gradient measures direct selection on each character after the effects of indirect selection on correlated characters have been removed. Selection gradients are estimated as

the standardized partial regression coefficients for each character generated from a multiple regression of relative fitness on the phenotypic characters entered (Arnold and Wade 1984a, 1984b). Highly correlated characters which are also correlated with fitness make calculation of selection gradients difficult (Lande and Arnold, 1983). For this reason it was decided to choose one of two traits, either fighting ability or weight, for the multiple regressions. Weight was used because many previous studies, involving a wide variety of organisms, as well as Gryllus, have measured selection on body size (reviewed in Endler 1986; French and Cade 1989; Cade and Cade 1992). Insect weight is often used as an indicator of general body size. Statistical significance of all selection gradients was determined using two-tailed t-tests. The R^2 values generated from the multiple regressions indicate what proportion of the observed matings can be explained by the variables entered. Statistical significance of the R^2 values was determined using F-tests. A parametric correlation matrix of the variables used as correlates to fitness, was constructed to examine their inter-relationships. Statistical significance of these correlations was determined using F-tests.

RESULTS

Behavioral data were collected for both sexes throughout this study. In the following sections the behavioral data for males are presented. The female behavioral data are also presented, but in the appendix since these data do not bear directly on the hypotheses under study yet nonetheless they describe an important component of the mating system.

Weight

Male weight ranged from 306 to 741 mg. Male weight was not significantly different between the sex ratios (one-way ANOVA: $F=1.12$, $p=0.3$, $df=88$). Table 1 shows the mean weights of all males, arranged according to sex ratio.

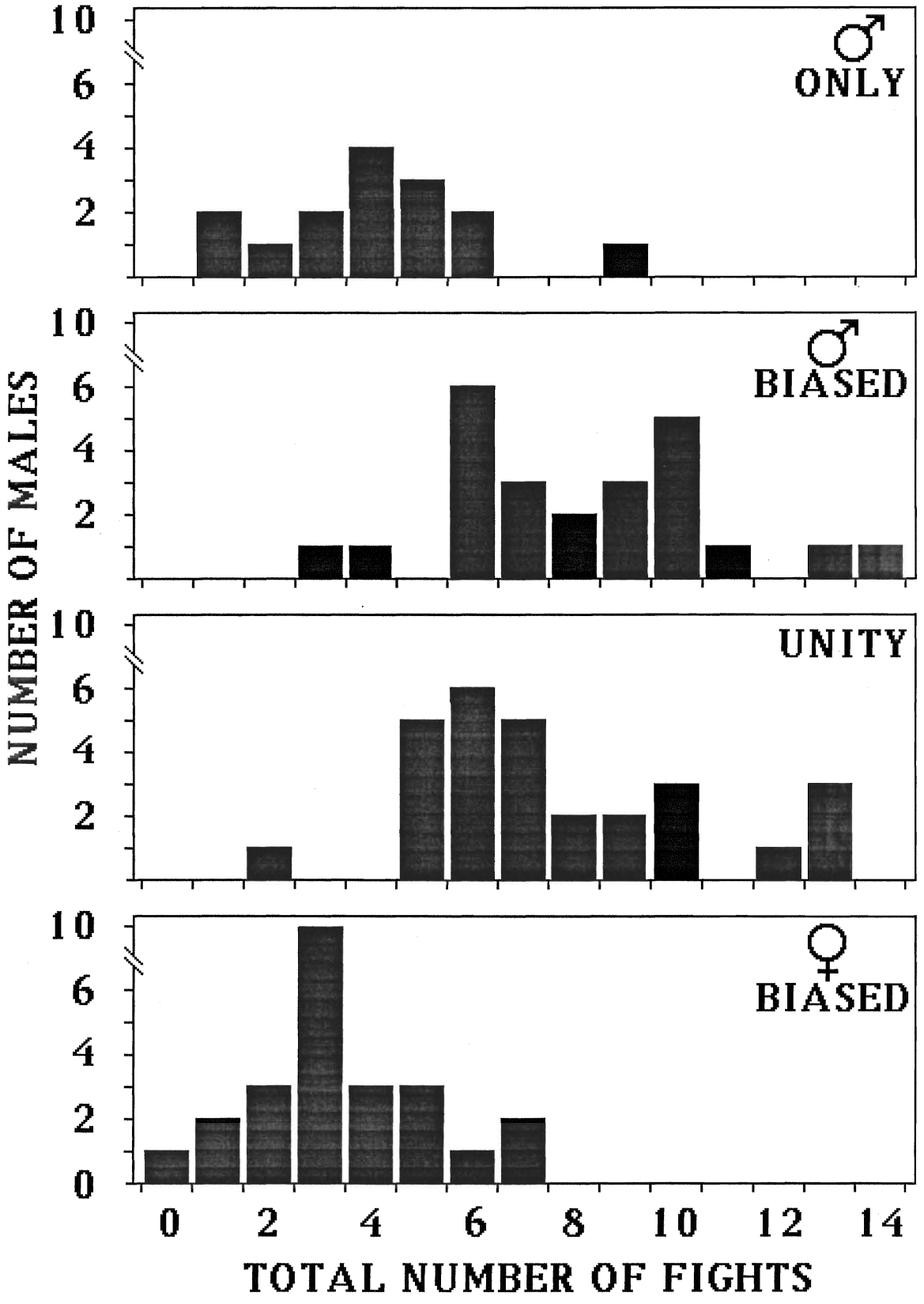
Frequency of Fighting

Frequency distributions of male aggressive interactions are included in figure 2. The mean number of fights (± standard deviation) per male over 30 hours at the 4 sex ratios are: 4.1±2.1 at male-only, 8.1±2.6 at male-biased, 7.8±2.9 at unity and 3.4±1.7 at female-biased. A significant difference in the frequency of these aggressive interactions was detected between sex ratios (one-way ANOVA: $F=22.17$, $p<0.0001$, $df=87$). Scheffe's F-tests indicated higher frequencies of fights at the male-biased sex ratio ($F=8.41$, $p<0.05$) and at unity ($F=7.30$, $p<0.05$), than when no females were present. Furthermore, significantly fewer fights occurred at the female-biased sex ratio than at the male-biased sex ratio ($F=14.42$, $p<0.05$) or at unity ($F=12.83$, $p<0.05$).

Table 1. The mean weight (±SD) arranged by sex ratio, of all males observed.

SEX RATIO	**5:0**	**5:2**	**5:5**	**5:10**
Male Weight (mg)	524±74	533±127	484±98	493±82

Figure 2. Frequency distributions of the total number of aggressive interactions by individual male G. pennsylvanicus over the 30 hour observation period at the different sex ratios.


10
6
4
2
♂
ONLY
10
6
4
2
♂
BIASED
10
6
4
2
UNITY
10
6
4
2
0
♀
BIASED
NUMBER OF MALES
0
2
4
6
8
10
12
14
TOTAL NUMBER OF FIGHTS

Weight and Fighting Ability

Table 2 displays correlation coefficients of male weight correlated against fighting ability at the 4 sex ratios. Male fighting ability (defined as % wins) was significantly correlated to male weight at all sex ratios (male-only; $F=10.26$, $p=0.007$, $df=14$: male-biased; $F=13.54$, $p=0.001$, $df=23$: unity; $F=19.76$, $p=0.0002$, $df=24$: female-biased; $F=34.03$, $p<0.0001$, $df=23$).

Calling Duration

The frequency distributions of the total time spent calling by males at the different sex ratios are presented in figure 3. At the male-only sex ratio males averaged (± standard deviation) a total of 369±223 minutes of calling over the three nights. Mean calling duration at the other sex ratios was 257±159 min. at the male-biased sex ratio, 209±162 min. at unity and 130±85 min. at the female-biased sex ratio. A significant difference in calling scores was detected (one-way ANOVA: $F=5.51$, $p=0.002$, $df=85$). Using Scheffe's F-tests for pairwise comparisons within model I ANOVAs, it was found that calling at the male-only sex ratio was significantly greater than calling at unity ($F=3.17$, $p<0.05$), or at the female-biased sex ratio ($F=4.93$, $p<0.05$).

Male Searching

Figure 4 displays frequency distributions of male searching distance across the 4 sex ratios. Males searched (± standard deviation) a total of 61.0±33.7 meters at the male-only sex ratio, 49.4±22.6 m at the male-biased sex ratio, 49.9±20.5 m at unity and 28.6±13.1 m at the female-biased sex ratio. A significant difference in male searching between the sex ratios was detected (one-way

Table 2. Parametric correlation coefficients of weight against fighting ability (% wins) across all 4 sex ratios.

SEX RATIO	5:0	5:2	5:5	5:10
r-value	0.66 * n=15	0.62 * n=24	0.68 * n=25	0.78 * n=25

* significant at $p<0.05$ using F-tests

Figure 3. Frequency distributions of total calling duration for individual male G. pennsylvanicus over the 30 hour observation period at the different sex ratios.

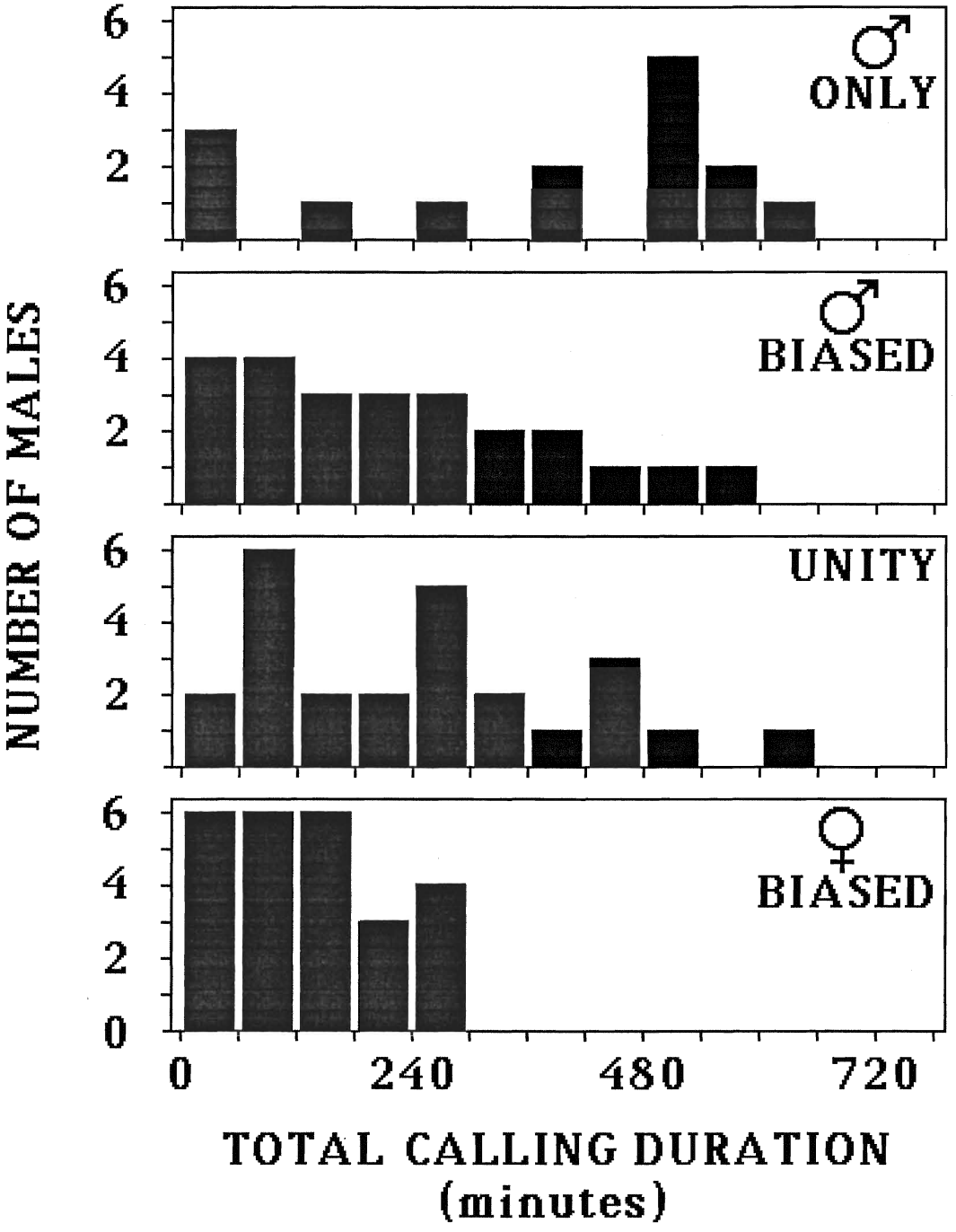
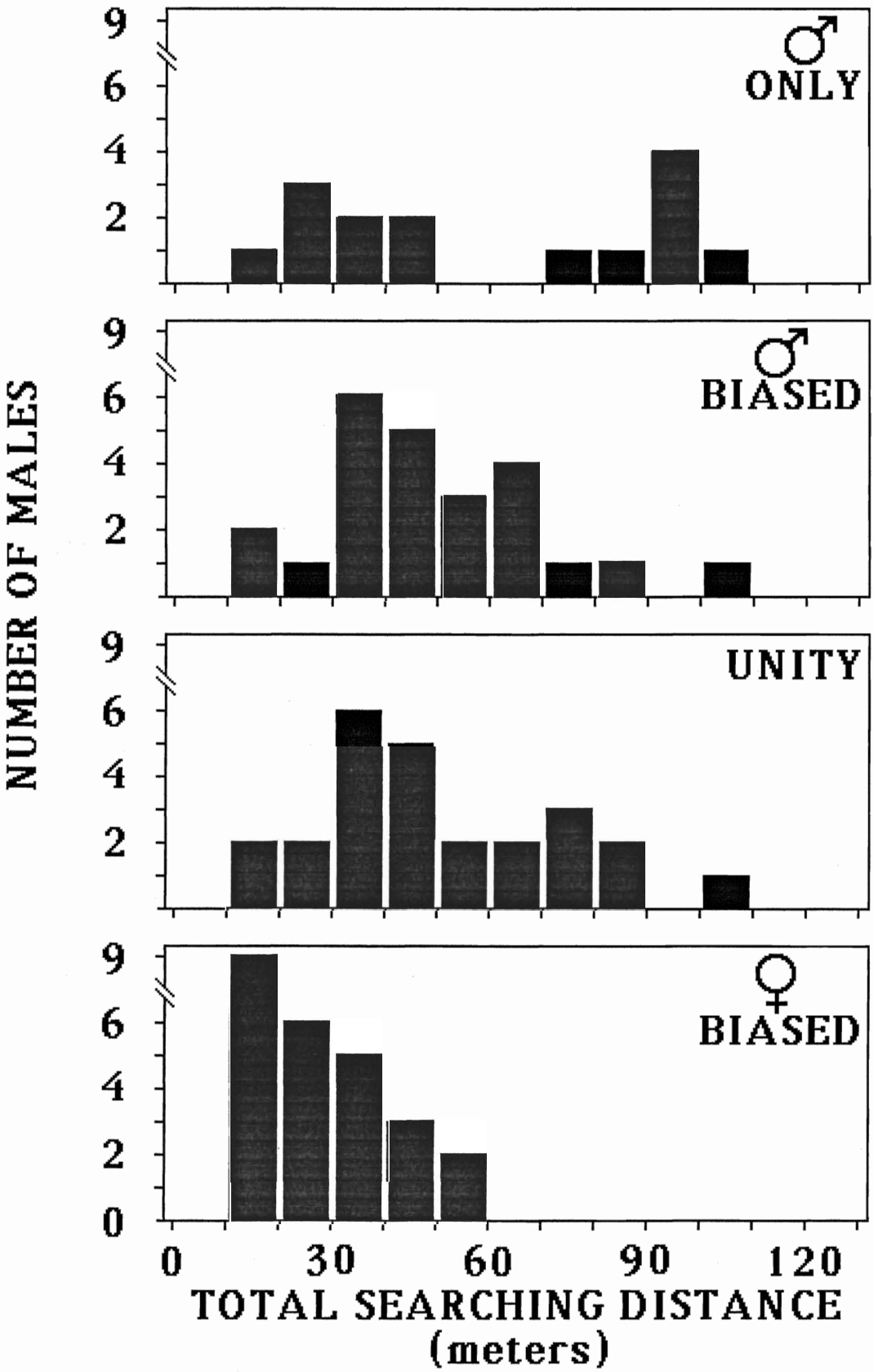

NUMBER OF MALES
6
4
2
♂ ONLY
6
4
2
♂ BIASED
6
4
2
UNITY
6
4
2
0
♀ BIASED
0
240
480
720
TOTAL CALLING DURATION
(minutes)

Figure 4. Frequency distributions of total searching distance for individual male G. pennsylvanicus over the 30 hour observation period at the different sex ratios.


NUMBER OF MALES
9
6
4
2
♂
ONLY
9
6
4
2
♂
BIASED
9
6
4
2
UNITY
9
6
4
2
0
♀
BIASED
0
30
60
90
120
TOTAL SEARCHING DISTANCE
(meters)

ANOVA: F=8.17, p<0.0001, df=88). Scheffe's F-tests indicated significantly less searching occurred at the female-biased sex ratio than at unity (F=3.99, p<0.05), than at the male-biased sex ratio (F=4.60, p<0.05), or than when no females were present (F=5.55, p<0.05).

Male Courtship Frequency

Figure 5 displays frequency distributions of the total number of courtships achieved by individual males across the 3 sex ratios. At the male-biased sex ratio males averaged (± standard deviation) 4.2±2.3 courtships over the 30 hours, 7.1±3.2 at unity, and 6.7±3.5 at the female-biased sex ratio. A significant difference was detected in courtship frequency for males (one-way ANOVA: F=5.11, p=0.009, df=72). Scheffe's F-tests for pairwise comparisons showed that the only significant difference lay between the male-biased sex ratio and unity, with males courting more at the latter (F=4.62, p<0.05).

Mating Frequency and the Opportunity for Sexual Selection

The frequency distributions of the total number of matings per male across the three sex ratios are presented in figure 6. Table 3 contains the mean male mating frequencies across these sex ratios as well as estimates of the opportunities for sexual selection. Mean number of matings was significantly different between the three sex ratios (one-way ANOVA: F=3.48, p=0.04, df=65). More matings occurred at the female-biased sex ratio than at the male-biased sex ratio (F=3.37, p<0.05). The adult sex ratio manipulation employed in this study, also, had a significant effect on the opportunity for sexual selection (one-way ANOVA: F=5.54, p=0.02, df=14). The opportunity for sexual selection was higher at the male-biased sex ratio than at

Figure 5. Frequency distributions of the total number of courtships by individual male G. pennsylvanicus over the 30 hour observation period at the different sex ratios.

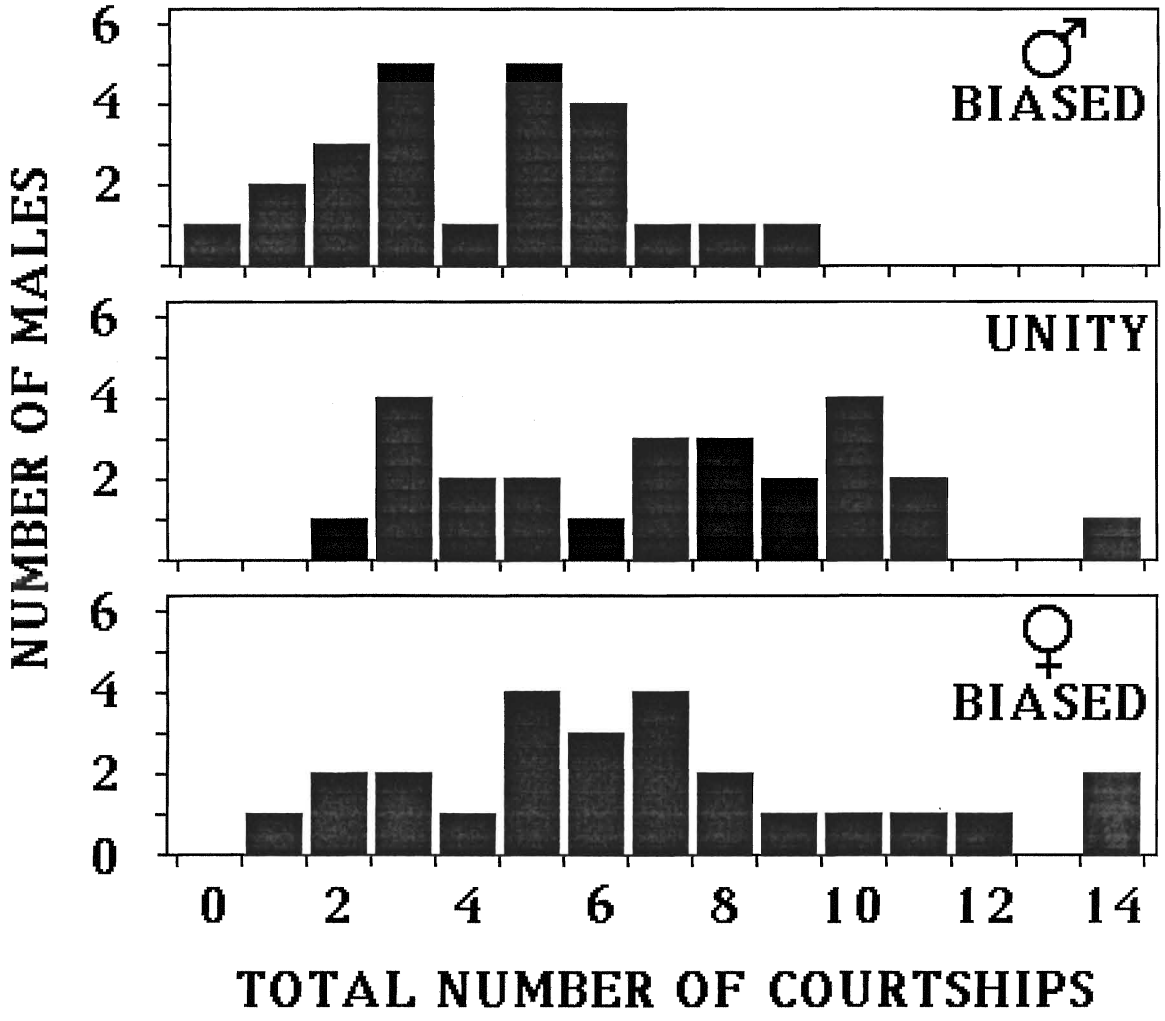

NUMBER OF MALES
6
4
2
♂
BIASED
6
4
2
UNITY
6
4
2
0
♀
BIASED
0
2
4
6
8
10
12
14
TOTAL NUMBER OF COURTSHIPS

Figure 6. Frequency distributions of the total number of matings by individual male G. pennsylvanicus over the 30 hour observation period at the different sex.

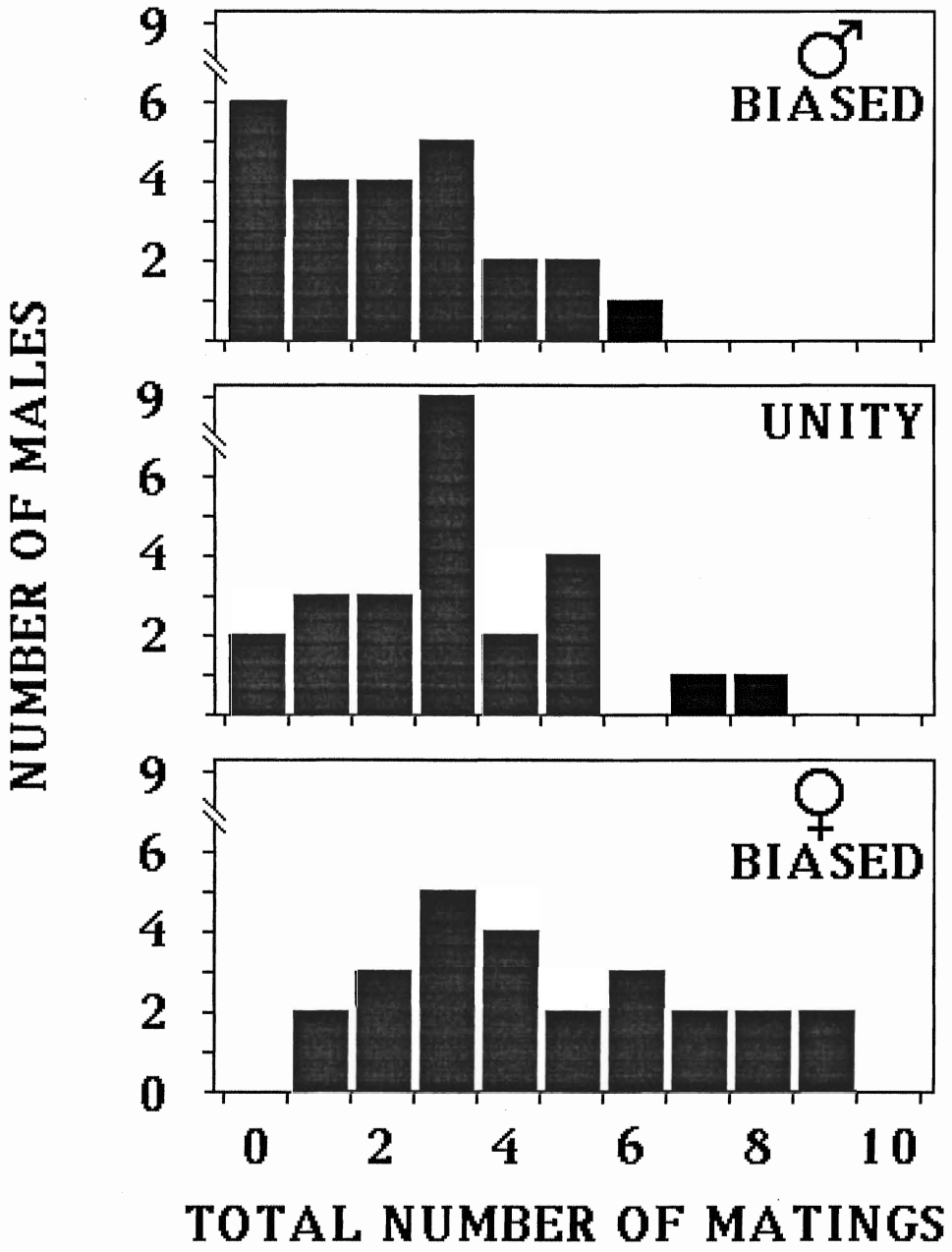

NUMBER OF MALES
9
6
4
2
♂
BIASED
9
6
4
2
UNITY
9
6
4
2
0
♀
BIASED
0
2
4
6
8
10
TOTAL NUMBER OF MATINGS

Table 3. Mean male mating success and the opportunity for sexual selection at the different sex ratios.

SEX RATIO	MALE BIASED 5:2	UNITY 5:5	FEMALE BIASED 5:10
Mean Male Mating Success (# of spermatophores attached in 30 hrs ± variance)	2.13±3.25 n=24	3.16±3.81 n=25	4.60±5.83 n=25
Opportunity for Sexual Selection (mean standardized variance of male mating success: I ± SD)	0.85±0.27	0.42±0.35	0.30±0.18

male-biased sex ratio than at the female-biased sex ratio ($F=5.03$, $p<0.05$).

Intervariable Correlations

Table 4 displays the parametric intervariable correlation matrix for weight, calling and searching across all 4 sex ratios. Weight and calling were not significantly correlated at the male-only sex ratio ($F=0.50$, $p=0.5$, $df=12$), or at the male-biased sex ratio ($F=0.50$, $p=0.5$, $df=23$), or at the female-biased sex ratio ($F=1.06$, $p=0.3$, $df=23$). Weight and calling however, were significantly correlated at unity ($F=5.16$, $p=0.03$, $df=24$). None of the correlations between weight and searching proved to be significant: male-only ($F=0.94$, $p=0.4$, $df=14$); male-biased ($F=0.07$, $p=0.8$, $df=23$); unity ($F=0.75$, $p=0.4$, $df=24$); and female-biased ($F=0.21$, $p=0.7$, $df=24$). Calling and searching, which represent two distinct male tactics for obtaining mates, showed negative but non-significant trends at all sex ratios: male only ($F=1.65$, $p=0.2$, $df=12$), male-biased ($F=3.06$, $p=0.09$, $df=23$), unity ($F=2.33$, $p=0.1$, $df=24$) and female-biased ($F=0.09$, $p=0.8$, $df=23$).

The Operation of Sexual Selection

Table 5 contains the selection differentials and the selection gradients for males at all the sex ratios where females were present. At the male-biased sex ratio the selection differential for calling was significant ($t=2.37$, $p=0.03$, $df=23$). Selection differentials for weight and for searching were not significantly different from 0 at the male-biased sex ratio (weight; $t=1.93$, $p=0.07$, $df=23$: and searching; $t=0.40$, $p=0.7$, $df=23$). The selection gradients at this sex ratio for both weight and calling were significant (weight; $t=2.64$, $p=0.02$, $df=22$: and

Table 4. Parametric correlation matrix of male characters at the 4 sex ratios investigated.

		WEIGHT		CALLING
	SR			
CALLING	5:0	0.21		
	5:2	-0.15		
	5:5	0.43*		
	5:10	0.21		
	SR		**SR**	
SEARCHING	5:0	0.26	5:0	-0.36
	5:2	0.06	5:2	-0.35
	5:5	-0.18	5:5	-0.30
	5:10	0.10	5:10	-0.06

* $p<0.05$ F-test

Table 5. The selection differentials, selection gradients, and multiple regression coefficients, for the 3 male characters across sex ratios. Male fitness was estimated as the number of spermatophores attached in 30 hours.

SEX RATIO	VARIABLE	SELECTION DIFFERENTIAL [1] ±SE	SELECTION GRADIENT [2] ±SE	R^2
MALE	Weight	0.32±0.16	0.38±0.14 *	0.413
BIASED	Calling	0.41±0.17 *	0.50±0.17 *	p=.01
n=24	Searching	-0.07±0.18	0.07±0.15	
UNITY	Weight	0.25±0.12 *	0.14±0.13	0.299
	Calling	0.30±0.11 *	0.22±0.13	p=.05
n=25	Searching	-0.17±0.12	-0.08±0.12	
FEMALE	Weight	0.09±0.11	0.22±0.12	0.250
BIASED	Calling	-0.18±0.11	-0.23±0.11 *	p=.12
n=25	Searching	-0.01±0.11	-0.04±0.10	

1 univariate regression coefficient between relative fitness and the character of interest

2 standardized partial regression coefficient generated from a multiple regression of relative fitness on each character of interest

* $p<0.05$ two tailed t-tests

calling; t=2.96, p=0.01, df=22). The selection gradient for searching was not significant at the male-biased sex ratio (t=0.45, p=0.7, df=22). The R^2 value generated from the multiple regression at the male-biased sex ratio was significant (F=4.70, p=0.01, df=23) and indicated that weight, calling and searching accounted for 41.3% of the variation in male mating success.

The selection differentials for weight (t=2.13, p=0.04, df=24) and for calling (t=2.68, p=0.01, df=24) were significant at unity. The selection differential for searching however, was not statistically significant (t=1.36, p=0.2, df=24). All three selection gradients at this sex ratio were not significant (weight; t=1.15, p=0.3 df=23: calling; t=1.67, p=0.1, df=23: and searching; t=0.65, p=0.5, df=23). The R^2 value generated from this multiple regression approached significance (F=2.98, p=0.054, df=24) and indicated that 29.9% of male mating success at unity could be successfully explained by the three variables.

All three selection differentials were not significant at the female-biased sex ratio (weight; t=0.87, p=0.4, df=23: calling; t=1.72, p=0.1, df=23: and searching; t=0.07, p=0.9, df=23). The selection gradient for calling was negative and significant at the female-biased sex ratio (t=2.153, p=0.0437, df=22). The selection gradients for weight and for searching, however, were not significant at this sex ratio (weight; t=1.87, p=0.08, df=22: and searching; t=0.41, p=0.7, df=22). The R^2 value obtained at the female-biased sex ratio was not significant (F=2.22, p=0.1, df=23) and indicated that only 25.0% of the variance in male mating success could be explained by the three traits.

DISCUSSION

The availability of mates can be an important factor in determining the structure of mating systems (Orians, 1961; Willson and Pianka, 1963; Emlen and Oring, 1977). This possibility has received substantial theoretical consideration, but empirical work on the effect of sex ratio on components of the mating system, is lacking. This study demonstrated that G. pennsylvanicus males respond behaviorally to changes in the availability of females. It was also shown that the sex ratio can affect the opportunity for selection as well as the intensity of selection operating on male traits. In this section, the results of a sex ratio manipulation experiment on the northern fall field cricket are discussed.

Effect of Sex Ratio on Gryllus Mating Behavior

Calling Frequency

In this study, male G. pennsylvanicus decreased the time they spent calling as the availability of females increased. Male calling behavior serves to attract females over relatively long distances (Alexander, 1961; Alexander, 1975; and Otte, 1977). Calling, however, is an energetically expensive male reproductive tactic (Prestwich and Walker, 1981), and if females are already present in the immediate vicinity in sufficient numbers persistent male calling may be maladaptive. Hence, as the availability of females increases, the amount of time a male spends calling might be expected to decrease. Energy and time that would have gone into calling, could be saved for other activities, or for calling when female availability decreases again. Male G. pennsylvanicus might detect changes in the

local sex ratio through prior mate encounter rates and adjust mean nightly calling duration accordingly. Pheromones may be important in male assessment of female availability. Sex recognition by short range pheromones has been demonstrated in Acheta domesticus and G. integer (Otte and Cade, 1976). Sexton and Hess (1968) suggested that such chemicals might help regulate the local distribution of house crickets, A.domesticus.

Searching Distance

In this study, male G. pennsylvanicus also decreased the amount of searching as the availability of females increased. When the operational sex ratio is male-biased, most males are expected to call. As the operational sex ratio becomes female-biased, the proportion of non-calling satellite males is expected to increase (Alexander, 1975 and Otte, 1977), and male searching should also increase. Therefore, one would expect to see the occurrence of these two reproductive tactics, calling and searching, to respond in opposite directions as the availability of females increases. In computer simulations, as the sex ratio becomes more female-biased, the average number of mate encounters per male increases, but the rate of increase is significantly higher for satellites than for callers. In dense, female-biased conditions, satellite males should therefore have a distinct advantage (Rowell and Cade, in press). However, in the present study, male searching decreased with increasing female numbers. Close-range pheromones may help G. integer satellite males locate and intercept approaching females (Cade, 1979a). One reason that calling and searching did not respond in opposite directions to sex ratio as predicted, might be that at the female-biased sex ratio,

the arena became "saturated" with females. Once a male has encountered a female, it is unlikely he will continue searching until he has had a chance to court and possibly mate with that female. Therefore, in the female-biased situation, males reacted by showing generally less reproductive effort, regardless of which tactic they employed.

Frequency of Fighting

Rowell and Cade (in press) showed that the frequency of male-male encounters should increase as sex ratio becomes male-biased. Furthermore, satellite males should always be faced with higher male-male encounter rates than callers. Here, the mean number of fights per male was higher at unity and at the male-biased sex ratio, than at the female-biased sex ratio or when no females were present. These results are in partial agreement with Rowell and Cade's model, in that when females were present, males showed less aggression as the sex ratio became female biased. At the male-only sex ratio, however, levels of aggression were lower than predicted. Since fighting behavior in field crickets is energetically expensive and perhaps risky, it should be adaptive for males to fight only when necessary. In an extremely male-biased condition with no females, males may not engage in fights because there are no mating opportunities. At the male-only sex ratio, resources should be allocated toward attracting mates by calling, rather than competing for mates, by fighting. At the male-only sex ratio, males showed the most effort in finding mates, with most calling and searching observed in this study. Burk (1983) found a significant correlation between male fighting success and mating success in Teleogryllus

oceanicus. This result was due both to male-male competition and female mate choice. If females discriminate between potential mates on the basis of fighting ability, male fighting behavior also facilitates intersexual competition.

Previous studies have not measured the frequency of male fighting in response to a manipulated sex ratio. Alexander (1961) proposed that as density increased, levels of aggression should decrease. Although the sex ratio manipulation employed here affected the overall density, the sex ratio was the factor of primary importance. Here, male density was kept constant throughout. Therefore Alexander's rational cannot be used to make any predictions, and the effects seen on the frequency of aggressive interactions might be attributed largely to changes in the availability of females. In a female-biased condition, mating opportunities abound, so that costs of competing for mates through fighting behavior may not balance the gains.

Courtship Frequency

As the sex ratio becomes female-biased, mate encounters should become more frequent (Rowell and Cade, in press), and therefore courtship and mating frequency should increase. In this study, there was an increase in total courtships per male from the male-biased sex ratio to unity, but no further increase as the sex ratio became female-biased. Average male mating success showed an increasing trend, but was not significantly different between the 3 sex ratios. These results provide further support for the hypothesis presented earlier concerning the "saturation" of male mating effort at the female-biased sex ratio. In polygynous mating systems, males

usually court and mate as often as opportunities present themselves or as often as they physiologically can. In the present study, about half of the courtships led to successful matings at the male-biased sex ratio and at unity. This increased to more than two-thirds at the female-biased sex ratio. These results suggest that there were fewer unsuccessful courtships at the female-biased sex ratio, indicating that females may have been less discriminating, or that it was easier for males to locate receptive females. Furthermore, there is some indication that males were more discriminating in the females they courted, ie. chosing to court heavier females (see appendix for details). Lawrence (1986) demonstrated that male milkweed beetles, Tetraopes tetraophthalmus became increasingly choosy when the sex ratio was female-biased. Shelly and Bailey (1992) showed that males of an undescribed Australian zaprochiline katydid species, were more likely to mate if they were exposed previously to a low mate encounter rate. If, however, they had been previously exposed to high mate encounter rate, not only were males more reluctant to mate, but they tended to reject lighter (less fecund) females. Female weight is known to be correlated to fecundity in a wide range of insects. However, no relationship was observed between female mating and female weight in this study (see appendix). These results suggest that sex ratio might also affect elements of intersexual competition.

Effect of Sex Ratio on the Opportunity for Sexual Selection

In the present study, a significant difference was detected in the opportunity for sexual selection between sex ratios, and pairwise comparisons determined that the opportunity for selection was

higher at the male-biased sex ratio than at the female-biased sex ratio. Furthermore, of the five I-values calculated for each sex ratio, the highest I-value overall occurred in the male-biased sex ratio and the lowest overall occurred in the female-biased sex ratio. These results provide strong empirical evidence for covariance between the operational sex ratio and the opportunity for sexual selection in a polygynous mating system. Direct measurements of the opportunity for sexual selection at different sex ratios are, for the most part, unknown. Under polygyny, variance in male mating success will set the upper limit for the opportunity for sexual selection because males realize greater variance in mating success (Clutton-Brock, 1988). If the operational sex ratio is biased towards males in a polygynous mating system, the variance in male mating success is expected to rise (Emlen and Oring, 1977), and therefore the opportunity for sexual selection will increase (Wade and Arnold, 1980; Lande and Arnold, 1983).

Thornhill was probably the first (unpublished, cited in Thornhill and Alcock, 1983) to provide some evidence for covariance between the operational sex ratio and variance in male mating success, in the scorpionfly, Panorpa. These scorpionflies form a mating system which may be classified as resource defence polygyny. Certain data from Kordic-Brown (1988) suggest that the standard deviation of male spawning success of pupfish, Cyprinodon pecosensis, covaries with sex ratio. The trend is more pronounced for satellite males than for territorial males in C. pecosensis, however, the statistical analysis used tested for differences between mean spawning success. Kordic-Brown did not directly apply these data to

the question of interest here, because she did not determine whether the variance in mating success was affected by sex ratio. Since these studies, the importance of skewed sex ratios in determining variance in reproductive success and thus the opportunity for sexual selection is for the most part uninvestigated empirically.

Effect of Sex Ratio on the Intensity of Sexual Selection

Selection differentials were used to measure total selection, or selection acting directly on a trait plus all indirect selection introduced by correlated traits. By going one step further and using the multivariate techniques of Lande and Arnold (1983), the confounding effects introduced by the correlated traits which have been measured, can be separated. This was done by calculating the selection gradients, which measure direct selection on each of the traits entered into the multiple regression.

Selection on Weight

Insect weight is often used as an indicator of general body size. In this study, male weight was correlated to male fighting ability, defined as percent wins, at all 4 sex ratios. Larger male G. pennsylvanicus appear to have a distinct advantage during fights. This relationship has been observed before in field crickets (Dixon and Cade, 1986). Therefore fighting ability is an important correlate of male weight. Although the multivariate regression is designed to handle correlated traits, problems arise when two strongly correlated traits are also correlated to the dependent variable (Lande and Arnold, 1983). For this reason it was decided to choose one of these two traits when measuring selection. Weight was chosen because

many previous studies, involving a wide variety of animals, have measured selection on body weight (Endler, 1986).

In this study, direct selection for increased body weight was detected at the male-biased sex ratio, while the selection differential was not significant. That is selection on weight alone (the effects of correlated traits neutralized) appeared stronger than total selection on weight. One way in which direct selection may appear to be stronger than total selection on a trait occurs if another trait correlated to mating success is negatively correlated to the trait of interest. A correlation matrix of all traits entered into the multiple regression becomes very useful in interpreting selection gradients and selection differentials. The intervariable correlation matrix showed that at the male-biased sex ratio, there was a non-significant negative correlation between weight and calling. Although this negative correlation was non-significant, it might have been sufficient to the extent that it increased the magnitude of the selection gradient for weight. The correlation between weight and searching was very weak at this sex ratio and probably did not appreciably influence total selection on weight, it is important to keep in mind however, that other traits correlated to weight and not measured during this experiment could affect selection on weight.

The direct selection detected at the male-biased sex ratio for weight indicates that body size was important in obtaining mates. In enclosures of crickets, male dominance hierarchies are frequently observed. Alexander (1961) observed male dominance hierarchies in an unidentified Gryllus sp. When such hierarchies are formed, it is expected that higher ranking males should realize higher mating

success than lower ranking males because dominant males can displace subordinates from females. Also females may prefer to mate with dominant males. Burk's (1983) work showed a correlation between male fighting ability and mating success, and demonstrates the dominant male advantage in acquiring mates. Furthermore, the declining frequency of fighting behavior as sex ratio became more female biased, demonstrated in the present study, indicates that fighting may be more important at the male-biased sex ratio and perhaps at unity than at the female-biased sex ratio, where fights were relatively infrequent. When the outcome of fighting behavior determines mating success, selection on body weight should be observed. Selection on body weight appeared greatest at the male-biased sex ratio in this study.

Selection for increased body weight was also detected at unity. But here, total selection for weight was statistically significant, while direct selection was not. This implies that another trait, which was positively correlated to weight, was also under selection (calling). At unity, weight and calling were positively and significantly correlated. When traits are associated in this way, total selection might be higher than direct selection for each. Larger, competitively successful males should be capable of defending calling sites and thus would spend more time calling. This appeared to be the case at unity here, but not at the male or female-biased conditions. Cade and Wyatt (1984) did not find a correlation between weight and calling duration in several Gryllus spp. including G. pennsylvanicus, but Cade and Cade (1992), using a relatively larger sample, did find a positive correlation, for G. integer at low population density.

Neither the selection differential nor the selection gradient for weight was significant at the female-biased sex ratio. French and Cade (1989), and Cade and Cade (1992) did not detect any selection on body weight in either G. pennsylvanicus, G. veletis, or G. integer. In both these previous studies, overall population density was manipulated, whereas here the sex ratio manipulation likely created an extremely competitive situation for males at the male biased sex ratio. The direct selection on weight seen here at the male-biased sex ratio indicates that in a highly competitive situation, the outcomes of fights played an important role in female mating decisions, and thus selection on male body weight occurred. The total selection seen at unity likely resulted from indirect selection introduced by the correlated trait, calling. Whereas selection on male body weight did not occur at the female-biased sex ratio because when mates are readily available, male-male confrontations are less common and apparently less important for obtaining mates.

Selection on Calling Duration

In this study, both total and direct selection were detected for increased calling duration at the male-biased sex ratio. The selection gradient for calling was larger than the selection differential, meaning that selection on calling alone (the effects of correlated traits neutralized) appeared stronger than total selection on calling. How this pattern may arise due to the effect of negatively correlated traits on selection was previously described for weight. Here, the apparently stronger direct selection than total selection for calling, may have been caused by the non-significant negative correlation between weight and calling. Selection on calling duration should be

related to the sex ratio. In male-biased conditions males call more, and those who call most should realize the greatest rates of mate encounter. Using computer simulations, Rowell and Cade (in press) showed that at male-biased sex ratios, calling males should experience greater rates of mate encounter than non-calling satellite males. Since calling song is primarily the way to attract mates over long distances, this tactic should be utilized when local mate availability is low.

At unity, total selection but not direct selection was detected for calling. This pattern may again have been caused by the correlated trait, weight. In this case, however, weight was a positively correlated trait which was also under total selection. Because these two traits, weight and calling, were positively correlated, total selection for each became significant, while direct selection for either was not significant because the effects of correlated traits had been removed. Both total and direct selection on calling appeared weaker at unity than at the male-biased sex ratio. These results indicate that the importance of calling song towards obtaining mates might have declined as the availability of mates increased. Rowell and Cade's model (in press) predicts that satellite behavior should lead to greater rates of mate encounter at unity than at a male-biased sex ratio. Therefore, a greater number of matings likely resulted from males adopting the satellite mating tactic at unity, lessening the advantage of calling evident at the male-biased sex ratio. Although there is no direct evidence, this hypothesis is supported by generally weaker selection on calling that was observed at unity.

At the female-biased sex ratio direct selection against increased calling duration was detected. Total selection however, was not statistically significant. This might have been caused by indirect selection introduced by the weakly correlated trait weight, whose selection gradient approached significance. That is, undetected selection for increased body weight, which was positively but non-significantly correlated to calling, may have offset total selection against calling. At the female-biased sex ratio, males that spent much of their time calling did not acquire many mates. This is reflected by the negative selection gradient. At extremely female-biased sex ratios and high population density, satellite behavior should attain a greater rate of mate encounter than calling behavior (Rowell and Cade, in press). At the female-biased condition here, it was demonstrated that males called substantially less, indicating the declining importance of calling as a mating tactic at female-biased sex ratios. The detection of negative direct selection on calling at the female-biased sex ratio, supports this hypothesis. Males that spent much time calling, did not mate very often. Calling behavior in this species, under conditions of high mate availability, appears to be maladaptive.

Selection on Searching Distance

No form of selection was detected for searching at any of the sex ratios. The selection gradients for searching were especially weak throughout. The selection differential at unity showed negative direction, but this may have been caused by the negative trends in correlations with both calling and weight. An increasingly female-biased sex ratio should lead to greater rates of mate encounter for

satellite males (Alexander, 1975; Rowell and Cade, in press), in which case searching should become the more beneficial reproductive tactic. The only observation supporting this hypothesis, in this study, is the occurrence of a negative selection gradient for calling at the female-biased sex ratio. This finding suggests that there is no benefit to calling at this sex ratio, but this does not serve as evidence for showing a direct benefit to searching. If a general reduction in male reproductive effort occurred at the female-biased sex ratio, selection on searching behavior may not have occurred because males would generally not have to move very far to obtain a mate, and would not necessarily improve their chances of finding a mate by searching over larger distances.

Other studies have shown that searching may not be a very important determinant of male mating success (French and Cade, 1989; Cade and Cade, 1992). Perhaps selection on searching was not detected here, because selection on searching might be much more subtle than selection on the primary mating tactic, calling. A wide range of selective regimes were observed for calling. In the G. pennsylvanicus mating system, the intensity of selection on calling alone may alternate from episodes of strong selection to episodes of weak selection in response to local mate availability. There may be no shift to selection for searching under such circumstances, selection on searching may not be dependent on local mate availability. Another possibility as to why no selection on searching was detected, concerns longevity and lifetime reproductive success. Perhaps the satellite mating tactic pays off because satellite males live longer than calling males, due to reduced predation rate, in which case data

on lifetime mating success might be required to detect selection on searching.

Searching, as measured in this experiment, may not have adequately quantified the male satellite tactic. In this study, searching was defined as the sum of hourly displacements. Although satellite males should show more searching simply because callers cannot move while calling, and because satellites are often displaced from a caller's territory, it may not necessarily quantify the male satellite tactic. Satellite males are not in constant random motion, rather, they strategically position themselves near the burrows of territorial males where they attempt to intercept females phonotactically attracted to the caller. They should avoid altercations with the caller, because if he stops calling, the advantages to adopting the satellite tactic quickly diminish. Satellites may remain at the fringe of a particular caller's territory for extended periods of time, and thus not amass a large searching score.

Population Density and the Sex Ratio

A number of experimental population density manipulations have been conducted in enclosures using field crickets. French and Cade (1989) found that both G. pennsylvanicus and G. veletis did not decrease nightly calling duration as population density increased. French and Cade's high density (0.12-0.14 males/m^2) compares well to the male density used throughout this study (0.12 males/m^2). Their high density G. pennsylvanicus males called 1.1 hours on average per night. In this study, males at unity called for a very similar duration of 1.2 hours on average per night. Cade and Cade (1992), however, found a significant decrease in calling in response

to increased density in G. integer, similar to the reduction in calling found in the present study. This southern species can reach extremely high densities, while G. pennsylvanicus is a moderate to high density species, and G. veletis is a low density species (Alexander and Meral, 1967). Unlike the two northern species, G. integer populations are composed of high proportions of macropterous individuals, and thus population density likely fluctuates more radically. Gryllus integer males may have evolved to be more responsive to subtle changes in mate availability because of the greater range of densities they encounter naturally. Cade and Wyatt (1984) showed that the coefficient of variation for calling duration was higher for G. integer than for G. pennsylvanicus or G. veletis.

Unlike the results discussed previously, where male searching decreased as the availability of mates increased, French and Cade (1989) found that mean male movement was not significantly different between high and low density in G. pennsylvanicus and in G. veletis. Since density is a more indirect way of manipulating mate availability, perhaps the range of densities used was not enough to elicit a response in this species. Another reason why French and Cade might not have observed an effect on movement concerns the densities used in their study. For these northern species, both high and low densities may have been near the extreme high that would be encountered naturally, and thus no difference in mean male movement was detected between them. In contrast, Cade and Cade (1992) showed that male G. integer moved more at high density than at low density. Since G. integer is a very high density species, and the

density manipulation was probably subtle enough not to "saturate" the male's ability to find mates, G. integer males may have adopted the predicted satellite tactic at the high density used.

Hissmann (1990) used natural variation to investigate the effects of population density on the behavior of G. campestris. At high density she observed equal numbers of calling males, silent males occupying burrows and searching males. Silent males occupying burrows had the highest rate of mate encounter. At low density, and a somewhat male-biased sex ratio, calling males were most numerous and also realized the highest rate of mate encounter. Evans (1983), Cade and Wyatt (1984) and Simmons (1986) had shown that field crickets are able to adjust their behavior in response to changes in population density. Hissmann's study is important because it suggests that this behavioral flexibility can also occur in the natural environment. She concludes by stating that age, sex ratio and density together may lead to the observed behavioral flexibility. Although sex ratio and density likely play large roles in determining behavior, age probably does not. Cade and Wyatt (1984) observed no change in individual calling duration in response to age, furthermore Hissmann did not individually identify any crickets, so there was no indication of age in her experiment, and no other studies have shown age dependent differences in behavior. In fact some laboratory studies have shown the converse (Souroukis et. al, 1992).

French and Cade (1989) and Cade and Cade (1992) did not detect any selection on body weight at high or low density in either G. pennsylvanicus, G. veletis, or G. integer. In this study, no selection

on body weight was observed at the female-biased sex ratio, but direct selection was detected at the male-biased sex ratio, probably because the condition created here was more competitive for males. Furthermore, total selection was detected for weight at unity. This, however, might have been largely due to the effect of the correlated trait calling, and therefore body weight was probably not the primary target of selection at unity.

French and Cade (1989) found that selection on calling duration occurred at low density but not at high density for G. pennsylvanicus. They found no selection on calling for G. veletis at high or low density. Cade and Cade (1992) also found that selection on calling duration occurred at low density but not at high density for G. integer. In the present study, selection on calling (direct and total) appeared greatest at the male-biased sex ratio, this and findings obtained in the density experiments, indicate that selection on calling can occur under conditions of low population density and male-biased sex ratios. Results also suggest that calling possibly becomes less important as a determinant of mating success at higher densities and at even sex ratios, and may even hinder a male's chances of mating under extremely female-biased conditions.

French and Cade (1989) found a positive selection gradient for searching at high density for G. veletis. However, no selection for searching in G. pennsylvanicus was detected. Cade and Cade (1992) found a negative selection differential for searching at low density using G. integer. The selection gradient, however, was not significant, and led them to conclude that the selection observed on searching at low density was the result of correlated traits. In this study, no

selection was detected on searching under any of the sex ratio regimes. G. veletis is naturally a very low density species, and in such species females may be less discriminating, due to low mate encounter rates. If G. veletis is placed under conditions of high population density, males may obtain more mates by increasing searching.

Conclusions

Male calling and searching were quantified as two behaviors important to the structure of the mating system. The proportion of time that males spend in each of these tactics appears to depend on population density (French and Cade, 1989; Cade and Cade, 1992). The present study suggests that sex ratio may also determine the proportion of time that males spend in each of these tactics. Here, correlations of calling against searching at all 4 sex ratios showed negative trends although none were significant. Cade and Cade (1992) found a significant negative correlation between calling and searching at low population density, but not at high density in G. integer. These male mating tactics are discrete, but conditional. Given the appropriate circumstances most males will adopt either tactic, and thus correlations of calling against searching need not always show significant negative associations. Therefore, when looking at behavior additively over a substantial proportion of the organism's life span, it is useful to treat these tactics as being continuously distributed traits (Cade, 1984).

Studies manipulate population parameters such as density and sex ratio because researchers view them as being real variables in the lives of animals, however field crickets may not assess and

change their behavior in accordance to these parameters, they may assess and respond to other variables such as mate encounter rate and rival encounter rate, which are related to both density and sex ratio. At present there is no indication as to how field crickets assess these external conditions. If mate encounter rate is being assessed, the operational sex ratio is a more direct measure of mate availability than population density. Therefore conditional male reproductive tactics should be more responsive to sex ratio manipulation, if the range of conditions is sufficient to elicit a response. This hypothesis is supported here by selection detected on calling. At the male-biased sex ratio, selection on calling was relatively strong, at unity no direct selection was detected, and at the female-biased sex ratio, direct selection on calling became significant and negative. Previous studies in which population density has been manipulated have not demonstrated this wide a range in the selective regimes of any particular trait. In these previous density manipulations one general trend has been observed. In field cricket mating systems, the general effect of increasing population density is to apparently weaken selection on male traits (French and Cade, 1989; Cade and Cade, 1992). A very similar effect was observed here for selection operating on the same 3 male traits; as the sex ratio became more female-biased, selection on male traits generally weakened.

Field cricket populations are structured such that spatial and temporal differences in the operational sex ratio can occur. These may occur due to differential predation and parasitism, sex biased aggregations, sex specific migratory behavior, and a variety of other

mechanisms. Veazey et. al. (1967) used pitfall traps to determine naturally occurring sex ratios of the field crickets, G. rubens, G. firmus and G. ovisopis. The proportion of males of all 3 species decreased in late summer or fall. Most of the sex ratios calculated were female-biased. Alexander (1968) stated that males are generally collected less frequently than females because males are generally less mobile and therefore less susceptible to the trapping method. Results obtained in the present study, however, indicate that male and female mobility is quite similar. Hissmann (1990) showed that over the course of one summer, population density decreased and the initial balanced sex ratio changed to a male-biased sex ratio, in G. campestris. Cade (1979b) demonstrated that flying G. integer were predominantly female, and when large flights occurred, they were characterized by large numbers of virgin females. Cade (1989) used calling males placed in an arena and taped calling song broadcast on a loudspeaker to attract flying G. integer. He found that significantly more females could be attracted this way, furthermore the number of crickets attracted each night as well as the proportion of males attracted, varied greatly. His results suggest that there exists great potential for temporal and spatial variation of local sex ratio in field crickets. Gwynne (1990) demonstrated that the abundance and quality of food available controls the operational sex ratio in the katydid, Requena verticalis. This study is interesting because it demonstrates how an external factor interacting with variation in parental investment between the sexes can produce skewed sex ratios.

The R^2 values generated from the multiple regressions indicate the proportion of all matings which are adequately described by the three independent variables. In density experiments the general trend has been for higher R^2 values at low density, in other words, at lower densities a greater proportion of matings can be accounted for by the independent variables. In this study, R^2 values showed a decreasing trend as the sex ratio became more female-biased. These trends suggest that the intensity of selection on male traits might covary with population density as well as with sex ratio. In this and previous studies, R^2 values have demonstrated that only a relatively small amount of the variation in male mating success can be attributed to the variables studied. A wide variety of unmeasured variables likely contribute to the remaining observed variance in mating success. Several aspects of calling song such as intensity (Cade, 1979a), bout duration (Hedrick, 1986), and perhaps some finer aspects of song structure, may contribute to this variation. Zuk (1988) showed that more females are attracted to older G. pennsylvanicus males, although how females assess male age is not known. In any case, age represents another possible source of variation. Yet another source of variation may be introduced by gut parasites, gregarines. Zuk (1987) found that male G. pennsylvanicus with lower gregarine loads realized greater mating success. Genetic relatedness of mates may be an additional source of variation. The degree of genetic relatedness of potential mates is assessed by female G. bimaculatus, who prefer to mate with distant relatives (Simmons, 1991). The additional sources of variation listed above,

likely account for some of the undescribed variance in male mating success, but certainly not all.

Heritabilities of male traits important in reproduction, have not been demonstrated for G. pennsylvanicus, however estimates are available for a number of other closely related field crickets. Heritability for calling duration has been estimated at around 0.5 in G. integer (Cade, 1981). Significant heritability for a number of body size indicators, was demonstrated in the field cricket G. bimaculatus (Simmons, 1987a). It seems quite reasonable that significant heritability for these traits will also exist in G. pennsylvanicus, but there is no direct evidence. Not much is known about the heritability of searching behavior, however there may be a significant genetic component to this trait as well.

In this study it was demonstrated that variation in sex ratio affects the opportunity for sexual selection and perhaps the intensity of selection acting on calling duration and male weight. Strong, constant directional selection should result in reduced additive genetic variation in the heritable characters targeted by such selection (Williams, 1975; Taylor and Williams, 1982; Cade, 1984). Selection, however, is not a constant force as so often assumed, and genotypes do not have constant fitness values (Kojima, 1971). If the strength of selection varies spatially and/or temporally for one reason or another, additive genetic variation should go through phases of high and low variation. Density-dependent and other fluctuations in selection may be responsible for the maintenance of much of the genetic variation underlying traits important in fitness (Kojima, 1971; Clarke, 1979). Data from insect and vertebrate

populations suggest that selection can become quite intense (Howard, 1983; Thornhill and Alcock, 1983; Price, 1984). Here it was shown that selection may be quite intense under some circumstances, yet quite relaxed at others. Cade (1984) suggested that density-dependent selection helped maintain genetic variation in G. integer reproductive behavior. Similarly, spatial and temporal variations in sex ratio may manifest as spatial and temporal fluctuations in the opportunity and intensity of sexual selection. The data presented here suggest that sexual selection on male G. pennsylvanicus traits important in obtaining mates may vary in intensity at different sex ratios. Thus, sex ratio heterogeneity should be categorized as an additional mechanism by which genetic variation in reproductive characters may be maintained.

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APPENDIX

Table 1. Raw data of all males used in this study. Weight was measured in milligrams; call, search, and total fights refer 30 hour totals, per male, for each of these behaviors (see methods for definitions). Percent wins refers to % of total fights won. Total court and total mate refer to the total number of courtships and matings by individual males. Females courted and females mated refer to the number of different partners obtained over 30 hours. The sex ratio, year and replicate are also reported.

male #	wgt	call	search	total fights	% wins	total court	fmles court	total mate	fmles mate	sex ratio	year /repl.
1	430	125	46.9	1	0	•	•	•	•	5:0	90/a1
2	435	520	37.4	2	0	•	•	•	•	5:0	90/a1
3	565	570	11.2	3	100	•	•	•	•	5:0	90/a1
4	480	0	29.0	3	0	•	•	•	•	5:0	90/a1
5	545	645	37.3	5	80	•	•	•	•	5:0	90/a1
6	519	520	26.6	6	33	•	•	•	•	5:0	90/a2
7	568	515	41.2	1	0	•	•	•	•	5:0	90/a2
8	547	50	87.9	6	50	•	•	•	•	5:0	90/a2
9	512	390	78.1	9	55	•	•	•	•	5:0	90/a2
10	438	520	25.4	4	75	•	•	•	•	5:0	90/a2
11	481	0	95.0	5	0	•	•	•	•	5:0	90/a3
12	611	545	96.6	5	80	•	•	•	•	5:0	90/a3
13	557	380	97.7	4	50	•	•	•	•	5:0	90/a3
14	704	490	104.8	4	100	•	•	•	•	5:0	90/a3
15	463	265	99.6	4	25	•	•	•	•	5:0	90/a3
16	417	165	46.7	6	0	4	2	2	2	5:5	90/b1
17	741	400	57.1	7	100	11	4	5	2	5:5	90/b1
18	596	230	55.6	13	38	9	4	3	2	5:5	90/b1
19	577	95	67.2	7	43	3	3	3	2	5:5	90/b1
20	560	190	46.5	13	62	10	4	3	2	5:5	90/b1
21	538	435	18.2	2	50	7	4	4	4	5:5	90/b2
22	541	490	32.2	7	86	10	5	4	3	5:5	90/b2
23	433	20	70.6	7	57	11	3	5	3	5:5	90/b2
24	489	30	73.3	13	46	8	3	3	2	5:5	90/b2
25	384	15	34.1	5	0	5	3	0	0	5:5	90/b2
26	550	180	36.6	10	70	7	3	1	1	5:5	90/b3
27	439	575	44.6	5	60	10	3	5	3	5:5	90/b3
28	361	45	39.7	5	40	8	2	3	1	5:5	90/b3
29	408	65	60.5	5	40	3	3	0	0	5:5	90/b3
30	432	30	63.9	6	33	10	4	1	1	5:5	90/b3
31	526	255	22.5	5	80	7	4	6	4	5:10	90/c1
32	626	225	13.4	2	100	6	3	5	2	5:10	90/c1
33	382	75	32.6	3	0	1	1	1	1	5:10	90/c1
34	464	80	36.7	4	0	3	2	3	2	5:10	90/c1
35	588	295	16.5	2	100	6	2	5	2	5:10	90/c1
36	369	30	18.6	5	0	4	3	2	1	5:10	90/c2
37	453	170	19.9	5	20	2	1	1	1	5:10	90/c2
38	511	20	18.4	3	100	10	5	8	3	5:10	90/c2

Table 1 continued.

male #	wgt	call	move	total fights	% wins	total court	fmles court	total mate	fmles mate	sex ratio	year /repl.
39	693	0	26.1	7	100	3	3	3	3	5:10	90/c2
40	588	130	47.7	6	50	8	6	4	3	5:10	90/c2
41	488	250	22.0	1	0	8	6	4	4	5:10	90/c3
42	501	95	23.4	3	100	12	6	7	4	5:10	90/c3
43	437	115	13.6	3	66	7	6	3	3	5:10	90/c3
44	377	120	30.1	1	0	5	3	3	3	5:10	90/c3
45	467	230	19.7	3	0	5	4	2	2	5:10	90/c3
46	427	280	38.5	6	33	3	2	1	1	5:2	90/d1
47	524	240	36.8	7	100	6	1	4	1	5:2	90/d1
48	306	125	48.5	10	0	2	2	2	2	5:2	90/d1
49	464	225	39.4	3	66	4	2	1	1	5:2	90/d1
50	394	190	65.9	10	50	2	1	0	0	5:2	90/d1
56	330	135	100.7	6	0	0	0	0	0	5:2	91/d2
57	428	325	33.2	6	16	1	1	0	0	5:2	91/d2
58	576	240	72.2	14	36	5	2	2	1	5:2	91/d2
59	613	105	87.2	10	80	5	2	3	2	5:2	91/d2
60	663	420	79.5	9	100	8	2	4	2	5:2	91/d2
61	373	410	15.5	4	0	2	1	0	0	5:2	91/d3
62	545	435	15.5	6	16	6	1	5	1	5:2	91/d3
63	598	355	40.3	10	80	5	1	3	1	5:2	91/d3
64	629	640	36.6	11	73	3	2	3	2	5:2	91/d3
65	712	115	65.4	7	29	3	2	2	1	5:2	91/d3
66	470	280	26.9	6	0	5	1	3	1	5:2	91/d4
67	721	80	51.5	9	44	3	2	2	1	5:2	91/d4
69	686	450	21.4	8	100	7	2	5	2	5:2	91/d4
70	619	110	37.6	7	43	3	2	0	0	5:2	91/d4
71	402	505	47.9	6	0	5	2	3	2	5:2	91/d5
72	624	5	55.5	10	50	6	2	0	0	5:2	91/d5
73	424	110	45.9	13	31	1	1	1	1	5:2	91/d5
74	566	290	81.5	9	66	9	2	6	2	5:2	91/d5
75	697	115	42.3	8	100	6	2	1	1	5:2	91/d5
76	403	250	38.9	7	0	7	5	4	3	5:10	91/c4
77	436	65	12.6	3	0	11	6	6	4	5:10	91/c4
78	533	85	34.5	3	100	14	7	9	6	5:10	91/c4
79	511	130	58.8	3	100	5	4	3	2	5:10	91/c4
80	576	210	55.2	4	100	2	1	2	1	5:10	91/c4
81	351	135	40.5	8	0	7	5	3	3	5:5	91/b4
82	409	125	28.5	10	40	2	2	2	2	5:5	91/b4
83	443	310	42.9	6	66	9	3	5	3	5:5	91/b4
84	421	385	50.1	12	83	4	3	2	2	5:5	91/b4
85	627	270	34.5	8	50	5	2	3	2	5:5	91/b4
86	360	285	89.0	6	0	6	4	3	2	5:5	91/b5
87	459	60	101.0	10	60	3	2	1	1	5:5	91/b5
88	523	340	63.7	6	83	8	4	7	4	5:5	91/b5
89	431	65	36.3	9	11	3	2	3	2	5:5	91/b5
90	604	275	15.5	9	100	14	5	8	4	5:5	91/b5

Table 1 continued.

male #	wgt	call	move	total fights	% wins	total court	fmles court	total mate	fmles mate	sex ratio	year /repl.
91	409	135	18.8	4	0	6	2	6	2	5:10	91/c5
92	446	145	23.2	0	•	7	4	7	4	5:10	91/c5
93	472	50	44.8	3	66	14	7	9	5	5:10	91/c5
94	499	25	41.4	2	50	9	6	8	5	5:10	91/c5
95	572	55	24.8	3	100	5	4	4	3	5:10	91/c5

FEMALE DATA

Figure 1 shows the 3 frequency distributions of female movement. A significant difference in mean female movement between the sex ratios was detected (one-way ANOVA: $F=5.18$, $p=0.008$, $df=82$). Scheffe's F-tests for pairwise comparisons showed that females moved significantly more at unity than at the female biased sex ratio ($F=4.93$, $p<0.05$). Within sex ratios mean mobility between the sexes is very similar (see results).

The courtship data appear in Table 2. Total courtship represents the mean number of courtships per male and per female, across the three sex ratios. Courting partners represents the mean number of different courting partners obtained by individual males and females, across the three sex ratios. Note that number of courting partners for males was directly manipulated in this study.

A significant difference was found in total courtship for females (one-way ANOVA: $F=21.29$, $p<0.0001$, $df=79$). Scheffe's F-tests showed that females participated in significantly less courtships at the female biased sex ratio than at unity ($F=10.33$, $p<0.05$), and than at the male biased sex ratio ($F=16.02$, $p<0.05$). A significant effect on number of courting partners obtained on the part of females was also found (one-way ANOVA: $F=13.24$, $p<0.0001$, $df=79$). Females participated in courtship with a larger variety of males at the male biased sex ratio ($F=9.47$, $p<0.05$) and at unity ($F=6.99$, $p<0.05$) than at the female biased sex ratio.

Figure 1. Frequency distributions of female movement for 30 hours across the 3 sex ratios that females were used. Means and standard errors are shown.

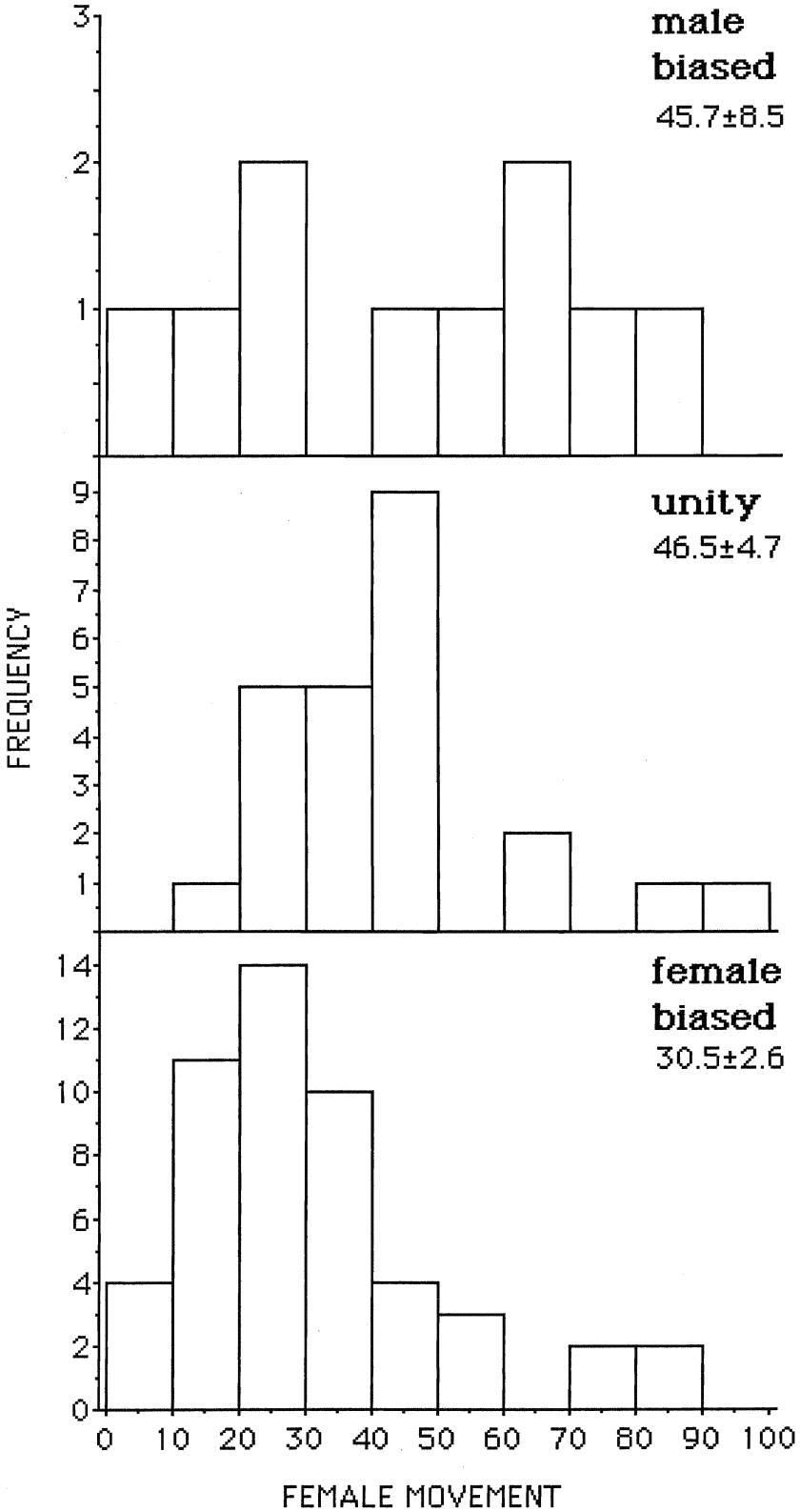
male
biased
45.7±8.5
unity
46.5±4.7
female
biased
30.5±2.6
FREQUENCY
FEMALE MOVEMENT
0
10
20
30
40
50
60
70
80
90
100

Table 2. The change in the mean frequency of female courtship behavior (±SE), in response to an experimentally manipulated sex ratio.

SEX RATIO	**5:2** n=10	**5:5** n=24	**5:10** n=49
Total Courtship	10.8(1.3)	6.8(0.6)	3.4(0.3)
Courting Partners	3.9(0.2)	3.3(0.2)	2.0(0.2)

The mating success data for females appear in Table 3. Total mating represents the mean number of matings per female, across the three sex ratios. Mating partners represents the mean number of different mating partners obtained by individual females, across the three sex ratios.

Total mating for females showed a significant effect (one-way ANOVA: $F=6.17$, $p=0.003$, $df=72$). Scheffe's F-tests showed that females participated in significantly more matings at the male biased sex ratio than at unity ($F=4.27$, $p<0.05$) and than at the female biased sex ratio ($F=6.05$, $p<0.05$). Mating partners for females was not significantly different between the sex ratios (one-way ANOVA: $F=2.62$, $p=0.08$, $df=72$).

An index of courtship for females (calculated: total courtships multiplied by courting partners) was significantly correlated with weight only at the female biased sex ratio ($r=0.34$, $F=5.7$, $p=0.02$, $df=45$), indicating that perhaps males chose to court heavier females at this sex ratio. Table 4 shows the weight of females used in this study arranged by sex ratio.

Table 3. The change in the mean frequency of female mating behavior (±SE), in response to an experimentally manipulated sex ratio.

SEX RATIO	**5:2** n=10	**5:5** n=24	**5:10** n=49
Total Mating	5.6(0.6)	3.2(0.4)	2.4(0.3)
Mating Partners	2.6(0.3)	2.1(0.2)	1.5(0.2)

Table 4. The mean weight (±SE) by sex ratio of all females observed.

SEX RATIO	**5:2**	**5:5**	**5:10**
Female Weight (mg)	692(68)	711(28)	722(22)

Table 5. Raw data for all females used in this study. Weight was measured in milligrams, total mate and total court refer to the total number of matings and courtships individual females obtained, males mate and males court refer to the number of different males that mated and courted individual females and movement is measured in meters. Column 8 gives the year and the replicate, column 9 indicates the sex ratio. Columns 3 to 7 are totals, over 30 hours of observation.

female #	wgt	total mate	total court	males mate	males court	move	year /repl	sex ratio
1	752	1	6	1	4	47.0	90/b1	5:5
2	836	5	8	4	4	44.0	90/b1	5:5
3	963	2	8	1	3	82.8	90/b1	5:5
4	558	1	5	2	1	28.7	90/b1	5:5
5	573	7	11	3	4	44.6	90/b1	5:5
6	794	4	11	3	5	49.2	90/b2	5:5
7	881	2	5	2	3	44.3	90/b2	5:5
8	778	1	5	1	3	45.3	90/b2	5:5
9	563	3	7	3	3	43.8	90/b2	5:5
10	707	6	11	3	4	29.8	90/b2	5:5
11	808	4	11	2	3	38.3	90/b3	5:5
12	541	1	7	1	4	45.4	90/b3	5:5
13	613	3	8	2	3	36.1	90/b3	5:5
14	651	0	1	0	1	32.1	90/b3	5:5
15	760	2	11	1	4	48.7	90/b3	5:5
16	674	5	5	1	1	32.0	90/c1	5:10
17	668	2	2	1	1	32.7	90/c1	5:10
18	351	2	3	1	2	44.2	90/c1	5:10
19	659	0	0	0	0	28.0	90/c1	5:10
20	620	2	2	2	2	27.0	90/c1	5:10
21	650	3	3	1	1	70.6	90/c1	5:10
22	828	1	1	1	1	35.0	90/c1	5:10
23	723	2	2	1	1	26.7	90/c1	5:10
24	696	0	0	0	0	42.5	90/c1	5:10
25	747	4	5	3	3	20.9	90/c1	5:10
26	641	4	4	2	2	19.9	90/c2	5:10
27	666	2	4	2	3	9.3	90/c2	5:10
28	409	1	1	1	1	16.5	90/c2	5:10
29	689	1	2	1	1	19.7	90/c2	5:10
30	630	0	0	0	0	30.8	90/c2	5:10
31	560	2	2	1	1	12.6	90/c2	5:10
32	823	3	7	2	4	4.4	90/c2	5:10
33	923	5	6	3	4	22.6	90/c2	5:10
34	784	0	1	0	1	33.2	90/c2	5:10
35	475	0	1	0	1	25.5	90/c2	5:10
36	1056	2	6	2	3	28.8	90/c3	5:10
37	783	4	4	4	4	13.6	90/c3	5:10
38	720	0	2	0	2	18.4	90/c3	5:10

Table 5. continued.

39	852	2	3	1	1	24.1	90/c3	5:10
41	601	1	2	1	1	21.5	90/c3	5:10
42	771	2	4	2	3	20.0	90/c3	5:10
43	1020	3	5	3	4	19.5	90/c3	5:10
44	809	2	4	2	2	33.0	90/c3	5:10
45	563	0	2	0	2	15.1	90/c3	5:10
46	698	2	4	2	3	19.1	90/d1	5:2
47	447	7	12	3	4	4.6	90/d1	5:2
50	876	4	10	3	4	83.6	91/d2	5:2
51	1042	4	7	2	3	66.9	91/d2	5:2
52	728	7	8	3	3	27.7	91/d3	5:2
53	605	6	10	1	4	74.9	91/d3	5:2
54	551	7	11	2	4	20.1	91/d4	5:2
55	805	8	17	3	5	52.3	91/d4	5:2
56	323	4	11	2	4	62.4	91/d5	5:2
57	846	7	18	5	5	45.8	91/d5	5:2
58	495	2	4	2	3	53.0	91/c4	5:10
59	815	6	8	2	3	30.1	91/c4	5:10
60	994	2	3	2	2	81.5	91/c4	5:10
61	691	6	9	3	4	53.9	91/c4	5:10
62	754	1	3	1	2	83.7	91/c4	5:10
63	627	2	3	2	2	40.6	91/c4	5:10
64	665	1	1	1	1	37.5	91/c4	5:10
65	740	4	6	3	3	33.3	91/c4	5:10
66	736	0	1	0	1	79.3	91/c4	5:10
67	863	2	4	1	3	41.9	91/c4	5:10
69	518	6	8	4	4	35.7	91/b4	5:5
70	649	2	3	2	2	22.0	91/b4	5:5
71	845	1	4	1	4	62.8	91/b4	5:5
72	941	1	2	1	1	20.3	91/b4	5:5
73	629	3	4	2	2	98.6	91/b5	5:5
74	732	2	5	2	3	107.1	91/b5	5:5
75	648	6	7	3	4	64.8	91/b5	5:5
76	797	8	9	4	4	28.2	91/b5	5:5
77	835	4	7	2	3	16.7	91/b5	5:5
78	845	4	5	3	3	13.0	91/c5	5:10
79	755	0	1	0	1	21.2	91/c5	5:10
80	850	5	5	2	2	59.2	91/c5	5:10
81	870	8	8	3	3	25.8	91/c5	5:10
82	658	5	5	3	3	24.7	91/c5	5:10
83	790	1	1	1	1	9.7	91/c5	5:10
84	376	1	4	1	1	11.7	91/c5	5:10
85	669	1	2	1	2	30.5	91/c5	5:10
86	677	5	6	3	3	22.6	91/c5	5:10
87	763	4	4	2	2	13.7	91/c5	5:10